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THE PHYSIOLOGICAL BALANCE OF NUTRIENT SOLUTIONS
FOR PLANTS IN SAND CULTURES

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By
ARTHUR G. McCALL

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PHYSIOLOGICAL BALANCE OF NUTRIENT SOLUTIONS FOR PLANTS IN SAND CULTURES¹

By

ARTUHR G. McCALL, *in Charge of Soil Investigations, Maryland Agricultural Experiment Station*

ABSTRACT

The experiments described in this paper were conducted for the purpose of studying the relative growth rates of young winter wheat seedlings, when grown in a substratum of sand and supplied with a nutrient solution of the same initial total concentration, but varying in the proportions of the component salts. An initial total concentration of 1.75 atmospheres maximum osmotic pressure was employed for 36 different proportions of the three component salts, KH_2PO_4 , $\text{Ca}(\text{NO}_3)_2$, and MgSO_4 .

The series included all of the possible proportions of the three salts, when the components are made to vary by increments of one-tenth of the total possible osmotic pressure. Each culture consisted of 6 plants growing in washed quartz sand. The enameled steel pots employed were approximately 12 x 12 cm., inside diameter, and held 1500 gm. of dry sand. After the seedlings were planted the surface of the sand was covered with a thin layer of wax to prevent loss of moisture by evaporation. The solutions were renewed every three days by the addition of 250 c.c. of fresh solution through a funnel which occupied a position at the center of the pot. At the same time that the fresh solution was being added at the top, the old solution was removed from the bottom of the pot by means of suction applied to a small tube connecting with the interior. The total growth period was 24 days, during which time the total water loss from each culture was determined at the end of each 3-day interval. At the end of the growth period the cultures were compared with respect to: (1) dry weight of tops, (2) dry weight of roots, (3) total water loss, (4) water requirement per gram of dry tops, (5) water requirement per gram of dry roots, and (6) the ratio of the weight of tops to dry weight of roots.

Three preliminary series of wheat cultures were grown in sand and supplied with nutrient solutions having a range in initial total concentration from 0.2 to 5.0 atmospheres. One of these series was characterized by having 5 tenths of the total osmotic concentration derived from monopotassium phosphate, 2 tenths from calcium nitrate, and 3 tenths from

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magnesium sulphate, while the other two had 4 tenths of the total osmotic concentration derived from KH_2PO_4 , 3 tenths from $\text{Ca}(\text{NO}_3)_2$, and 3 tenths from MgSO_4 . These three series were in accord in showing that a total concentration of 1.75 atmospheres was well within the range required for optimal growth of wheat tops.

The main results may be summarized as follows:

1. The graphs representing the growth rate of young wheat plants, for three preliminary series, show a region of optimal growth rate lying between the concentrations 1.0 and 2.0 atmospheres.

2. With the initial total concentration about 1.75 atmospheres, the nutrient solution that produced the greatest dry weight of tops also produced the greatest dry weight of roots. This solution is characterized by having 2 tenths of the total osmotic concentration derived from KH_2PO_4 , 7 tenths from $\text{Ca}(\text{NO}_3)_2$, and 1 tenth from MgSO_4 .

3. A general comparison of the results from this sand culture series with solution cultures (Shive's) grown from the same lot of seed but at a different time period brings out some interesting comparisons, which may be summarized as follows: (1) the average dry weights of both tops and roots were decidedly greater for the plants grown in the sand than for those grown in the solutions, (2) the results obtained in the solution culture series having a total osmotic concentration of 0.1 atmosphere, are more nearly like those from the sand series than are the results secured from the more concentrated solution series (1.75 atm.) in which the solutions were of the same total osmotic concentration as that employed for the sand cultures, and (3) there is a marked difference between the solutions producing the best development of plants in sand and those giving the best growth in the solution cultures, with respect to the osmotic proportions of the three salts employed.

4. A comparison of the results from these two series, the one grown in solution and the other in sand cultures, furnishes evidence for the conclusion that selective adsorption plays an important rôle in bringing about the observed physiological differences.

5. The sand culture solutions giving *low* yields of tops are characterized by a *wide* range in the Mg/Ca ratio; a very wide range in the Mg/K ratio, and a narrow range in the Ca/K ratio value. The solutions giving *high* yields of tops show a *narrow* range in the Mg/Ca ratio; and a comparatively wide range in both the Mg/K and Ca/K ratio values.

6. The data presented support the conclusion of earlier workers to the effect that the total transpirational loss from a plant culture is approximately proportional to the growth made by the plants during the period of time considered.

7. The water requirement per gram of dry tops varies considerably with the different proportions of the component salts. From these data it appears that *low* water requirement for tops is associated with a *low*

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partial osmotic concentration of mono-potassium phosphate, and that *high* water requirement is associated with *high* partial concentrations of both magnesium sulphate and mono-potassium phosphate.

8. The water requirement per gram of dry roots is much higher than the same value for tops.

9. A consideration of the ratio of tops to roots brings out the fact that in every instance a high water requirement corresponds to a high ratio of tops to roots.

10. Good growth of tops was found to be associated with a high osmotic ratio of $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 and poor growth of tops with a low value of this ratio. We are not justified, however, in drawing, from these results, any definite conclusions with respect to the calcium-magnesium ratio as such, since much of the superior growth, in the cultures where $\text{Ca}(\text{NO}_3)_2$ was in excess, may be ascribed to the presence of a large amount of the NO_3 radical, which is known to be favorable to very vigorous vegetative growth.

INTRODUCTION

During the closing years of the seventeenth century Woodward (46) grew spearmint, potatoes and vetch in rain, spring, river, conduit and distilled water, for the purpose of determining whether it was the water or the solid soil particles which nourished plants. It appears, however, that water cultures were not employed for the purpose of studying plant nutrition to any great extent until about 1859, at which time Knop (16) and Sachs (32) began their investigations of Liebig's theory that the materials dissolved in the soil water are not generally sufficient for plant growth and that plants derive food directly from the soil particles.

This early work of Knop and of Sachs, together with their subsequent experiments along the same lines, gave such an impetus to water-culture work that there has grown up, during the past half century, a very extensive literature upon the subject of water or solution cultures. Most of the earlier publications in this field are to be found in *Die Landwirtschaftliche Versuchs-Stationen*, while a general review of the literature may be found in such works as those of Pfeffer (30), Duggar (9), and Czapek (7). The very recent work of Tottingham (40) and the publications of Shive (37, 38) have added a very important and interesting chapter to the already voluminous literature upon the subject of plant nutrition with special reference to the physiological requirements of the plant.

After an extensive chemical study of the components of a standard formula, Tottingham grew preliminary cultures of wheat in two forms of Knop's solution, one including mono-potassium phosphate and the other having the phosphate in the di-potassium form. In these cultures, the solution containing the mono-potassium phosphate produced 17.8

per cent better growth of tops and 17.5 per cent better growth of roots than the solution containing the di-potassium salt. Following this preliminary work, Tottingham employed 84 different solutions, all of approximately the same total osmotic concentration, but each culture differing from all of the others in the proportions of the four salts, mono-potassium phosphate, potassium nitrate, calcium nitrate, and magnesium sulphate. To each of the cultures was added the usual trace of iron, in the form of ferric phosphate. With a total concentration at about the optimum for young wheat seedlings, the solution having the proper salt proportions to give the best growth of tops was found to produce an improvement of 11 per cent, based on the dry weight of tops grown in Knop's solution of the same total osmotic concentration.

Repeating some of these tests, Shive obtained results that show a very close agreement with those previously reported. His best growth was secured with the same proportions of salts as those found best by Tottingham, and an improvement of 12 per cent over Knop's solutions was obtained.

As a result of the further study of these four-salt solutions, Shive has been able to make a combination of three nutrient salts which contain all of the essential elements of plant growth (with the exception of iron) and which does not form a precipitate in solutions of the required concentration. The solutions employed by this writer contain mono-potassium phosphate, calcium nitrate and magnesium sulphate, and differ from the four-salt solutions just mentioned by omission of potassium nitrate. The three salts dissociate in dilute solutions, to form all of the ions that are found in the four-salt mixture of Knop or Tottingham. Testing this three-salt solution by the same general method as was employed by Tottingham, Shive secured cultures showing an improvement of 27 per cent over Knop's solution of the same total concentration. With this series of wheat cultures was included Tottingham's best solution, which showed a corresponding increase over Knop's solution of but 16 per cent.

Upon learning of these recent results, the writer became greatly impressed with the desirability of studying the effect of these solutions upon plants grown in sand where some of the physical environmental conditions of the soil are present, but where the cultures are relatively unaffected by the biological complications introduced when ordinary soils are used. The work of Tottingham and that of Shive were confined exclusively to water cultures, in which the solution was renewed at frequent intervals. Accordingly, it was planned to repeat a part of the work of Shive, using the same three-salt solution as was employed by him and the same kind of plant (wheat), but employing pure sand as the substratum, instead of having the roots of the plants completely immersed in the free solution. In order to secure a renewal of the nutrient solu-

tions at intervals during the growth of the plant, a special method (25) was devised, whereby the old nutrient solution could be removed and fresh solution added to the pots, without seriously disturbing the relation between the roots and the sand.

This investigation was conducted in the Laboratory of Plant Physiology of the Johns Hopkins University, under the direction of Dr. B. E. Livingston, to whom the author is deeply indebted for many criticisms and helpful suggestions.

METHODS

I. Sand Cultures with Renewed Solutions

After a great deal of preliminary work, the following method was adopted as best suited to the needs of the experiment. The pots used were of enameled steel ("graniteware"), approximately 12 x 12 cm., inside diameter, narrowing slightly toward the base and having a wide projecting rim at the top. When filled to within about 3 cm. of the top, these pots hold 1500 gm. of dry quartz sand. To provide for the removal of the solution a small lead tube is soldered into the side as near the bottom as possible.¹ The soldered joint and the lead tube are covered with paraffin, to guard against possible lead-poisoning, and the outlet of the tube closed by means of a short length of rubber tubing provided with a pinch-cock. The accompanying photograph, Plate I, shows the form of the pot and gives a good general idea of the appearance of the cultures at a period of about 20 days after planting. The description of the method given in the following paragraphs includes the details of manipulation from the starting of the seedlings to the harvesting of the plants.

The seed is soaked in water and the seedlings grown, in the manner described by Tottingham, to a height of about 3 or 4 cm., when they are ready to be transferred to the sand cultures. While the seed is being germinated, 1500 gm. of dry quartz sand (previously washed several times with distilled water) are weighed into the pot, the outlet at the bottom of the pot being screened on the inside by means of a plug of glass wool inserted before the pot is filled. With the pinch-cock closed, distilled water is now added to the pot until the sand is completely saturated, after which the pinch-cock is opened and the surplus water allowed to drain out through the tube at the bottom of the pot, until the last free water has disappeared from the surface of the sand. An inverted hemispherical porcelain funnel is placed in position at the center of the soil surface, as shown in Plate I, and the pot is then ready to receive the seedlings.

After careful selection for uniformity, the seedlings (six in number)

¹ In order to make the hole in the side of the pot it is necessary first to chip off a small piece of enamel with the sharp point of a file. This serves to give entrance to the point of a small twist drill which then passes through the iron and chips off the enamel on the inside, thus exposing sufficient iron to give adherence to the solder.

are planted, being equally spaced on a circle lying midway between the edge of the funnel and the wall of the pot. Care is taken to place the seedlings at such depth that the top of the grain is just level with the surface of the sand. After all of the seedlings are in place, the pinch-cock is closed, and the pot is tapped gently on the table until free water appears on the surface of the sand. This manipulation serves to pack the sand around the roots of the seedlings and at the same time to level the surface of the sand preparatory to putting on the seal of Briggs and Shantz (4) wax. This wax is composed of 80 per cent paraffin and 20 per cent petrolatum, the exact proportions being unimportant. The mixture has such a low melting point and is such a poor heat conductor that it can be poured around the most delicate seedlings without injury.¹ The surplus water is then drawn out of the pot by application of suction (by means of a water-aspirator) to the tube at the bottom, and a thin layer of the melted wax is flowed over the surface, completely covering the sand between the funnel and the wall of the pot. Care should be taken to have the wax only a few degrees above its melting point or the seedlings may be injured at the point of contact with the wax. The surface must be sealed to prevent the loss of water by evaporation from the surface of the sand, and, of course, the walls of the pot must be impervious to moisture in order that transpiration can be measured and the concentration of the nutrient solution controlled.

The pot is now ready to receive the nutrient solution, which is added through the funnel at the top while the water is being removed at the bottom by the application of suction to the outlet tube. A double or triple portion of the nutrient solution is passed through the sand at this first application, in order to flush out the distilled water. The pot is now placed on the balance and the removal of solution is continued until the sand has been reduced to the desired moisture content, which should be, as nearly as possible, the optimum for plant growth. At the end of each 3-day period the pot is again weighed, and sufficient water is added through the funnel to bring the entire system back to its original weight. A fresh nutrient solution is then added (250 c.c. for pots of this size), while an equivalent quantity of solution is removed at the bottom. A nutrient solution of the same concentration may be used throughout the entire period of growth, or it may be varied from time to time as the plants continue to develop. The plants may be harvested at any time by removing the wax seal and cutting them level with the surface of the sand. If desired, the roots may be recovered from the sand by washing them out with a jet of water. The records of pot weights give the amount

¹ The writer has found the paraffin sold under the trade name "Parawax" to be cheap and very satisfactory. Care must be taken to secure a good grade of petrolatum or vaseline. Some brands seem to contain volatile substances which cause injury to the plants at the point of contact with the seal. The Chesebrough brand of white vaseline has been found to be safe to use for this purpose.

of water lost by each culture (transpiration) and the harvest records may be made to include the dry weights of both tops and roots.

II. Materials Used

The substratum used in these cultures consisted of medium-fine white sand,¹ which had been previously washed four times with distilled water from a Barnstead still. For the first washing a 2-gallon glazed stoneware jar was filled about two-thirds full of distilled water and the dry sand slowly poured in while the contents of the jar were kept agitated by means of a large glass stirrer. The surplus water was then decanted, after which the sand was spread out on large sheets of paper until air-dry. The dry washed sand was then weighed into the granite-ware pots and was afterwards washed three times by covering with distilled water and drawing the water through the material by means of suction applied to the tube at the bottom of the pot. Failure of control cultures to develop in the sand supplied only with distilled water, instead of with the nutritive solution, gave conclusive proof that this washing treatment was sufficient to remove any nutrient salts that might have been in the unwashed sand.

The salts used in making up the culture solutions were Baker's "analyzed" mono-potassium phosphate and calcium nitrate and Merck's "blue label" magnesium sulphate. Stock solutions were prepared by dissolving gram-molecular weights of the salts separately in Jena flasks, each solution being made up to a volume of one liter. Before making up the final nutrient solutions the stock solutions were diluted to one-fourth molecular and stored in flasks, each of the latter being connected to a burette with automatic filling arrangement. By means of these burettes the required amounts of solution were drawn at each time when a new set of nutrient solutions were to be prepared. The drying of the salts, the making up of the stock solutions, and all of the other manipulations with respect to the making up of the nutritive solution were substantially the same as those described by Shive (38).

III. Culture Solutions

The growth-rate of a plant is determined by two sets of conditions, one of which is internal to the plant and hence thus far very largely beyond our control, while the other is external, or environmental, and hence subject more or less to artificial control. In the present work an attempt

¹ A mechanical separation of this sand gave the following percentages of different sized particles:

| Fine Gravel (2.0 to 1.0 mm.) | Coarse Sand (1.0 to 0.5 mm.) | Medium Sand (0.5 to 0.25 mm.) | Fine Sand (0.25 to 0.1 mm.) | Very Fine Sand (0.1 to 0.05 mm.) |
|---------------------------------|---------------------------------|----------------------------------|--------------------------------|-------------------------------------|
| 0.14 | 48.62 | 26.40 | 22.88 | 1.46 |

was made to have the internal conditions of the various plants as nearly uniform as it was possible to make them, by starting a large number of seedlings and selecting plants of uniform size and appearance. The environmental conditions may be further divided into two groups, one of which may be defined as aerial and the other as subterranean. Since the present study concerns the subterranean environment it was essential that the aerial environment should be made as uniform as possible for all of the cultures. This uniformity in aerial conditions is best secured by placing the cultures on rotating tables, as described by Shive, thus exposing all of the plants to approximately similar changes of heat, light, and moisture conditions. However, since rotating tables were not available for this work, a less convenient method was employed: the cultures were shifted in position each day, in regular order, on a stationary table. In order to avoid unequal shading, as far as possible, the cultures were placed in two single rows extending east and west in the greenhouse, the rows being of sufficient distance apart so that at no time during the day was there any shading of one row by the plants in the other. As a further precaution, each row of pots stood on narrow slabs of slate which were elevated about 15 cm. above the general level of the table.

In studying the comparative physiological effects of different nutrient solutions in such cultures as these, it is of course desirable to have uniformity in all of the subterranean conditions affecting the plant, excepting those conditions that are dependent upon the properties of the nutrient solutions, but this is difficult of accomplishment. A fairly satisfactory degree of uniformity in the subterranean physical conditions was secured by filling all of the pots from the same bulk sample of sifted sand and by taking care to maintain the same amount of moisture in all of the pots throughout the duration of the experiment. As has been pointed out by Livingston (18) and others, the cultural solution may influence the plant in two different ways. The chemical effect of the solution is dependent upon the chemical nature of the salts present and also upon the relative amounts of the different salts contained in the nutrient solution. On the other hand, the solution may exercise a marked influence upon plant growth in a purely physical way, by virtue of its total concentration to which is related the osmotic equilibrium between the nutrient solution outside the roots and the cell sap within. When water cultures are employed, the total concentration of the solution with which the roots are in contact is known with a fair degree of accuracy, but in sand cultures the solution may undergo a change not only in its total concentration but also in the relative proportions of the different salts, as the result of its contact with the solid particles of the substratum.

Elaborate investigations concerning the relation between the concentration of the solution in the soil and the growth of plants have resulted in disappointment largely because of the fact that, while it has been admitted that the adsorbed layer at the immediate surface of the soil grain

is of different concentration from that of the mass of free solution, it appears that no method has yet been devised for determining this difference in concentration. Furthermore, no direct experimental evidence has been reported that would throw light upon the question of the availability and the non-availability of salts in the adsorbed layer. It has been suggested that the thickness of the adsorbed layer is frequently less than that of the outer cell walls that cover the absorbing protoplasm in epidermal cells of roots. From this, it is argued that, since the protoplasm does not come into direct contact with the adsorbed layers about the soil grains, this layer, therefore, must be unavailable to the plant except for the possible slow diffusion of the salts from the adsorbed layer out into the adjacent free-water film. As a further support for the theory that the adsorbed layer is not available to plants, it is pointed out that the addition of a few pounds of a soluble potash salt to an acre foot of soil, for instance, often produces a very decided increase in the growth of the crop, although there may be present in the upper foot of soil as much as 10,000 pounds of potassium. This is interpreted to mean that the salt originally present in the soil solution was practically all in the adsorbed layers and that the relatively slight addition resulted in increasing the concentration of the free solution.

The effect of adsorption in reducing the toxicity of certain dissolved substances has been observed by several investigators.

True and Oglevee (41) studied the effect of the addition of difficultly soluble substances to toxic electrolytes and non-electrolytes. Sand, filter paper and paraffin were added to dilute solutions of the toxic substances and the changes produced by the addition of these materials were detected by observing the growth rate of the primary root of *Lupinus albus* when emersed in the different solutions for a period of 24 hours. The presence of these insoluble substances in the toxic solutions always gave an accelerated growth rate, the effect being quite similar to that produced by simple dilution. These investigators regard it as probable that the substances added to the toxic solutions acted as adsorbing surfaces for the molecules or the ions of the toxic substances dissolved in the liquid. This would affect the solution much like the addition of water, to bring about a decreased number of molecules or ions in a given volume of free solution. Similar results were obtained by Breazeale (2).

In a paper under the same title published the following year, these last mentioned authors (42) cite the work of Nägeli, with *Spirogyra* growing in distilled water obtained from copper containers. Nägeli (27) had found that his solutions, containing minute traces of a toxic metal, could be made harmless by the addition of paraffin, graphite, filter paper, or glass.

Dandeno (8) has also studied the effect of the addition of finely divided soils to toxic solutions. He found that the effect of the addition of non-chemical bodies to toxic solutions very much retarded the action

of the toxic substances in bringing death to the radicles of plants growing in such solutions.

Jensen (15) has shown that the introduction of pure quartz flour into a toxic solution reduces its toxicity to a marked degree. He states, however, that it is an open question whether the reduction in toxicity is due (1) to adsorption, (2) to reduced freedom of movement of the solute particles (that is, a reduction of the diffusion rate), or (3) to possible chemical changes induced by the presence of the finely divided quartz.

Breazeale (1) quotes some of Livingston's unpublished data, to show that in soil or in sand cultures the effect of concentration is quite different from that found in water cultures. These data indicate that the concentration best suited to the growth of wheat in water cultures is about 300 parts per million, while in sand cultures the solution giving the best growth rate has an initial concentration of approximately 2500 parts per million.

The present investigation furnishes some very important evidence concerning the availability of the adsorbed salts, which evidence will be discussed after the experimental results have been presented.

Following the nomenclature employed by Tottingham (40) and Shive (38), the concentrations used will be expressed in terms of osmotic concentration (maximum osmotic pressure in atmospheres¹), or in terms of gram-molecules per liter of solution.

EXPERIMENTATION

I. Determination of the Optimal Total Concentration

Working with water cultures, Tottingham (40) secured his best growth of wheat seedlings in a solution having a total osmotic concentration of 2.50 atmospheres, but he calls attention to the fact that this concentration may be somewhat above that required for optimal growth, and Shive (38) has shown that a total concentration of 1.75 atmospheres of maximum osmotic pressure lies within the range of concentration required for the best growth of wheat seedlings.

To determine if these approximately optimal total concentrations, found for water cultures, would hold good for sand cultures, three preliminary series of sand cultures were grown. The cultures of each series all received solutions having the same proportions of the three component salts, but the total osmotic concentration of the solution used was different for the various individual cultures in the same series. These preliminary cultures will be designated as Series A, Series B, and Series C. Series A and B were grown simultaneously from April 9 to April 29, while Series C was started April 28 and harvested May 18. Each series consisted of 6 cultures, differing from each other, as has been mentioned, in the total concentration of the nutrient solution employed, but all cultures

¹For a discussion of the methods used for measuring the physical properties of solutions, and an explanation of the terms employed, see Findlay, Alexander (10), Washburn, E. W. (43).

in the same series having the same salt proportions. The solutions for Series A ranged in concentration from a minimum of 0.5 of an atmosphere to a maximum of 3.0 atmospheres, and were further characterized

TABLE I

DRY WEIGHTS OF TOPS OF WHEAT GROWN FOR 20 DAYS IN SAND, WITH THREE-SALT SOLUTIONS VARYING IN TOTAL CONCENTRATION FROM 0.5 TO 3.5 ATMOSPHERES

Series A, conducted from April 9 to April 29, 1915

| Culture No. | Total Concentration of Solution | Amount of Molecular Solution Required per Liter of Nutrient Solution | | | Dry Weights | |
|-------------|---------------------------------|--|-----------------------------------|-------------------|-------------|-----------------------|
| | | KH ₂ PO ₄ | Ca(NO ₂) ₂ | MgSO ₄ | Absolute | Relative to Culture 1 |
| | atm. | c.c. | c.c. | c.c. | gm. | |
| 1 | 0.5 | 5.1 | 1.5 | 4.3 | 0.8022 | 1.00 |
| 2 | 1.0 | 10.2 | 3.0 | 8.6 | 1.0498 | 1.31 |
| 3 | 1.5 | 15.3 | 4.5 | 12.9 | 1.0998 | 1.37 |
| 4 | 2.0 | 20.4 | 6.0 | 17.2 | 1.2454 | 1.55 |
| 5 | 2.5 | 25.5 | 7.5 | 21.5 | 1.0006 | 1.25 |
| 6 | 3.5 | 35.7 | 10.5 | 30.1 | 0.8678 | 1.08 |

by having 5 tenths of the total osmotic concentration derived from mono-potassium phosphate, 2 tenths from calcium nitrate, and the remaining 3 tenths from magnesium sulphate. The solutions employed in Series B

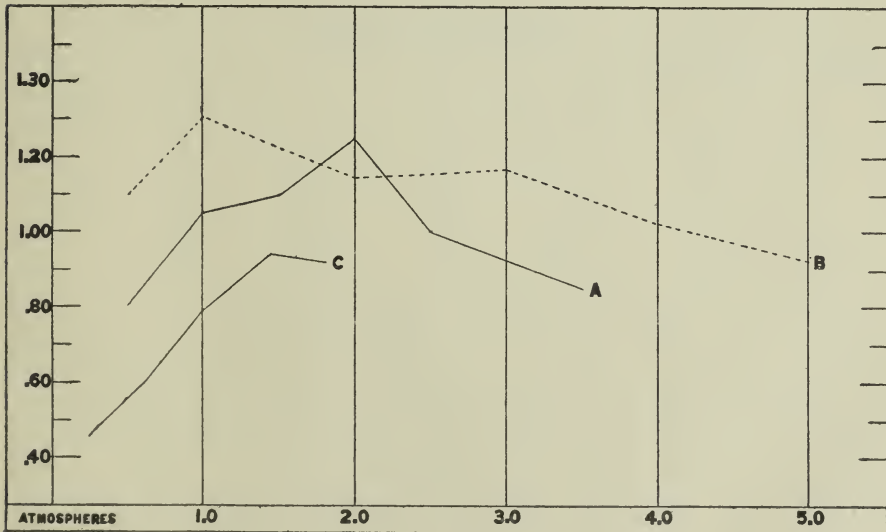


Fig. 1.—Dry weights of wheat grown for 20 days in sand cultures, with a three-salt solution varying from 0.1 atmosphere to 5.0 atmospheres total osmotic concentration.

had a range in total concentration from a minimum of 0.5 of an atmosphere to a maximum of 5.0 atmospheres, and derived 4 tenths of the total concentration from mono-potassium phosphate, 3 tenths from calcium

nitrate, and 3 tenths from magnesium sulphate. In Series C the solution ranged in total concentration from 0.2 of an atmosphere to 1.8 atmospheres, with the relative proportions of the three salts the same as in Series B. These particular sets of salt proportions were selected for the preliminary series because of the fact that Shive had already shown that these are associated with high yields of tops in solution cultures.

The data concerning the yield of tops in these preliminary series are given in Tables I, II and III. In these tables the first column gives the culture numbers; the second column shows the total concentration of the solutions employed, stated (in terms of maximum osmotic pressure) as atmospheres or fractions of an atmosphere. The three succeeding columns show, in each instance, the volume of stock molecular solution necessary for a liter of the required nutrient solution. Then follow two columns, one of which is devoted to the absolute, and the other to the relative dry weights of tops, the latter expressed in terms of Culture 1,

TABLE II
DRY WEIGHTS OF TOPS OF WHEAT GROWN FOR 20 DAYS IN SAND, WITH THREE-SALT SOLUTIONS VARYING IN TOTAL CONCENTRATION
FROM 0.5 TO 5.0 ATMOSPHERES

Series B, conducted from April 9 to April 29, 1915

| No. Culture | Total Concentration of Solution | Amount of Molecular Solution Required per Liter of Nutrient Solution | | | Dry Weights | |
|-------------|---------------------------------|--|-----------------------------------|-------------------|-------------|-----------------------|
| | | KH ₂ PO ₄ | Ca(NO ₃) ₂ | MgSO ₄ | Absolute | Relative to Culture 1 |
| | atm. | c.c. | c.c. | c.c. | gm. | |
| 1 | 0.5 | 4.6 | 2.5 | 5.3 | 1.1074 | 1.00 |
| 2 | 1.0 | 9.2 | 5.0 | 10.6 | 1.3347 | 1.21 |
| 3 | 2.0 | 18.4 | 10.0 | 21.2 | 1.1430 | 1.03 |
| 4 | 3.0 | 27.6 | 15.0 | 31.8 | 1.1749 | 1.06 |
| 5 | 4.0 | 36.8 | 20.0 | 42.4 | 1.0210 | .92 |
| 6 | 5.0 | 46.0 | 25.0 | 53.5 | 0.9256 | .84 |

taken as unity. The relative dry weights obtained in these series are shown in the graphs of figure 1. From an inspection of the graphs it will be seen that (with the osmotic proportions of the three salts here employed) the best growth of tops in sand cultures was obtained by the use of nutrient solutions with total concentration between 1 and 2 atmospheres. Since the concentration of Shive's optimal water-culture solution (1.75 atm.) is within the range of optimal concentrations as shown by these preliminary sand cultures, that concentration was employed in the subsequent work here to be reported.

II. *Determination of the Effect of Thirty-six Different Salt-Proportions, with the Total Concentrations and Other Conditions Alike*

Following the preliminary work recorded in the previous section of this paper, wheat plants were grown in a complete series of sand cultures, to each pot of which was added, at 3-day intervals, a three-salt nutrient solution. The method by which the old solution was withdrawn and the fresh solution added to the pots has already been described. In this series, 36 cultures were employed, each of which received at the end of successive 3-day periods a culture solution having a total osmotic concentration of 1.75 atmospheres. The solution supplied to each particular culture differed, however, from that supplied to the other cultures in the series, with respect to the proportions of the three main component salts, mono-potassium phosphate, calcium nitrate, and magnesium sulphate.

TABLE III

DRY WEIGHTS OF TOPS OF WHEAT GROWN FOR 20 DAYS IN SAND, WITH THREE-SALT SOLUTIONS VARYING IN TOTAL CONCENTRATION FROM 0.2 TO 1.8 ATMOSPHERES

Series C, conducted from April 28 to May 18, 1915

| Culture No. | Total Concentration of Solution | Amount of Molecular Solution Required per Liter of Nutrient Solution | | | Dry Weights | |
|-----------------|---------------------------------|--|-----------------------------------|-------------------|-------------|-----------------------|
| | | KH ₂ PO ₄ | Ca(NO ₃) ₂ | MgSO ₄ | Absolute | Relative to Culture 1 |
| | atm. | c.c. | c.c. | c.c. | gm. | |
| ¹ 0A | H ₂ O | | | | .1547 | |
| 0B | H ₂ O | | | | .2260 | |
| 1A | 0.2 | 1.8 | 1.0 | 2.1 | .4580 | } ² 1.00 |
| 1B | 0.2 | 1.8 | 1.0 | 2.1 | .4526 | |
| 2A | 0.6 | 5.4 | 3.0 | 6.3 | .6234 | } ² 1.32 |
| 2B | 0.6 | 5.4 | 3.0 | 6.3 | .5804 | |
| 3 | 1.0 | 9.0 | 5.0 | 10.5 | .7910 | 1.73 |
| 4 | 1.4 | 12.6 | 7.0 | 14.7 | .9368 | 2.06 |
| 5 | 1.8 | 16.2 | 9.0 | 18.9 | .9180 | 2.00 |

¹ Culture number 0 received only distilled water in this series. Cultures 0, 1 and 2 were in duplicate, each pair being indicated by A and B.

² Mean from two cultures.

The method of calculation by which the partial osmotic concentration and the volume-molecular concentration of each component salt in mixtures such as this, with a fixed total osmotic concentration, has been discussed by Tottingham (40, p. 177-182, 192), in connection with his four-salt solutions. In calculating the amount of each salt required to produce the total concentration required by the series (1.75 atm.) it was assumed that the degree of ionization of each salt is independent of the presence of the other two salts. In other words, the assumption was here made that each of the three salts would behave, in the presence of the other two, in the same manner as it would if dissolved in distilled water. The lowering of the freezing-point was determined by Shive (36) for each

one of the three-salt solutions employed by him, and it appeared from these determinations that the freezing-point lowerings were approximately the same for all of the solutions of his optimal series. Since Shive's series of optimal solutions are the ones here employed, it may safely be concluded that the *initial* total osmotic concentration of the nutrient solutions used in these sand cultures very closely approximated 1.75 atmospheres.

Table IV gives the volume-molecular concentrations of each salt required to produce from 1 tenth to 8 tenths of the total osmotic concentration for the various solutions in the series under consideration, these being taken from Shive's Table I (36, p. 339). To determine the volume molecular partial concentration of any given salt in any solution of this series it is only necessary to find, in the first column of this table, the number of tenths of the total concentration to be assigned to that particular salt, and then to take from the proper column the volume molecular concentration given opposite this number.

TABLE IV
VOLUME-MOLECULAR PARTIAL CONCENTRATIONS REQUIRED TO PRODUCE FROM FROM 1 to 8 TENTHS OF THE TOTAL OSMOTIC CONCENTRATION FOR A SERIES OF SOLUTIONS HAVING A TOTAL CONCENTRATION OF 1.75 ATMOSPHERES

| Tenths of Total Concentration | Partial Concentrations in Gram Molecules per Liter | | |
|-------------------------------------|--|----------------------------|-----------------|
| | KH_2PO_4 | $\text{Ca}(\text{NO}_3)_2$ | MgSO_4 |
| 1 | 0.0036 | 0.0026 | 0.0050 |
| 2 | 0.0072 | 0.0052 | 0.0100 |
| 3 | 0.0108 | 0.0078 | 0.0150 |
| 4 | 0.0144 | 0.0104 | 0.0200 |
| 5 | 0.0180 | 0.0130 | 0.0250 |
| 6 | 0.0216 | 0.0156 | 0.0300 |
| 7 | 0.0252 | 0.0182 | 0.0350 |
| 8 | 0.0288 | 0.0208 | 0.0400 |

For convenience in designating the individual cultures and to give clearness to the following discussions, the cultures may be arranged on an equilateral triangular diagram, as was done by Shive for his similar series. This diagram is shown in figure 2, and in another form in figures 3, 5 and 8. Similar graphic schemes have been used extensively in chemical interpretation, and have been employed by Schreiner and Skinner (33, 34) and by Tottingham (40), as well as by Shive (38) and by Harris (13). The individual cultures are represented by circles, and it will be observed that the diagram has eight rows, the lower one of which contains eight individual cultures. Proceeding upward each row has one culture less than the one below it, and the eighth row contains but a single culture. The employment of shaded segments to the various partial osmotic concentrations of the three salts, in each of the 36 cultures under consideration, is an adaptation of the scheme employed by Harris (13) in his study of the alkali salts in soils. The unshaded segment in each cir-

cle represents the number of tenths of the total osmotic concentration derived from calcium nitrate; the segment marked by small crosses represents the number of tenths derived from mono-potassium phosphate; and the stippled segment indicates the number of tenths due to magnesium sulphate. The system of numbering the individual cultures, and the corresponding nutrient solutions, is the same in figure 1 as that employed by Tottingham (40, p. 194) and by Shive (38, p. 341). Proceeding from the base to the apex of the triangle, the rows are numbered from R1 to R8, while the individual cultures in each row are numbered from left to right. For example, the fourth culture from the left in the second row from the base is designated R2 C4, and similarly the second culture in the seventh row is R7 C2.

The diagram of figure 2 shows that all of the solutions represented as in the first row have approximately 1 tenth of their total osmotic concentration from mono-potassium phosphate, those in the second row 2 tenths, this amount increasing by increments of 1 tenth from row to row, until the apex of the triangle is reached, at which point the single culture in row 8 has 8 tenths of its total concentration due to mono-potassium phosphate. As indicated by the shading, the first culture, at the *left* in each row, has 1 tenth of its total concentration due to calcium nitrate, and this partial concentration increases regularly by increments of 1 tenth until the opposite side of the diagram is reached. In a similar manner the osmotic partial concentrations of magnesium sulphate increase from *right* to *left* in each row. The circle occupying the position R1 C2 has 1 tenth of its total area unshaded, 2 tenths marked by crosses, and the remaining 7 tenths stippled, thus indicating that the solution used for this culture had the osmotic proportions of 1 tenth mono-potassium phosphate, 2 tenths calcium nitrate and 7 tenths magnesium sulphate. Throughout this paper the individual cultures will be designated by the row number and by the position occupied in the row, using the nomenclature employed by previous writers. The partial volume-molecular concentration of each salt in each of the 36 solutions is given in Table V, together with the corresponding values of the three cation ratios. Each solution has a total osmotic concentration of 1.75 atmospheres.

DISCUSSION OF RESULTS

I Introductory

The series of cultures which are now to be considered were grown in sand for a period of 24 days extending from May 15 to June 8, 1915. The wheat used was of the Fulcaster variety, from the same lot as was used by Tottingham (40) and by Shive (38), in their water cultures. As has already been stated, the methods employed for the germination of the seed and for the manipulation of the solutions were the same as those described by Shive (38), with such modifications as were made necessary by the employment of sand instead of water cultures. A detailed ac-

count of the method employed in the preparation of the sand and the manipulation used to secure a renewal of the solution at regular intervals has already been given.

TABLE V

PARTIAL VOLUME-MOLECULAR CONCENTRATION OF EACH OF THE SALTS IN EACH OF THE 36 THREE-SALT SOLUTIONS EMPLOYED FOR WHEAT IN SAND CULTURES; ALSO, THE THREE VALUES OF THE CATION RATIOS FOR EACH SOLUTION
Total concentration of each solution 1.75 atmospheres

| Solution Number | Partial Solutions in Gram-Molecules per Liter | | | Cation Ratio Values ¹ | | |
|-----------------|---|-----------------------------------|-------------------|----------------------------------|--------------|--------------|
| | KH ₂ PO ₄ | Ca(NO ₃) ₂ | MgSO ₄ | Mg — Ca | Mg — K | Ca — K |
| R1 C1 | .0036 | .0026 | .0400 | 15.40 | 11.10 | 0.72 |
| C2 | .0036 | .0052 | .0350 | 6.74 | 9.72 | 1.44 |
| C3 | .0036 | .0078 | .0300 | 3.85 | 8.34 | 2.16 |
| C4 | .0036 | .0104 | .0250 | 2.40 | 6.94 | 2.88 |
| C5 | .0036 | .0130 | .0200 | 1.54 | 5.55 | 3.60 |
| C6 | .0036 | .0156 | .0150 | 0.96 | 4.17 | 4.33 |
| C7 | .0036 | .0182 | .0100 | 0.55 | 2.78 | 5.04 |
| C8 | .0036 | .0208 | .0050 | 0.24 | 1.39 | 5.77 |
| R2 C1 | .0072 | .0026 | .0350 | 13.46 | 4.86 | 0.36 |
| C2 | .0072 | .0052 | .0300 | 5.77 | 4.17 | 0.72 |
| C3 | .0072 | .0078 | .0250 | 3.21 | 3.47 | 1.08 |
| C4 | .0072 | .0104 | .0200 | 1.92 | 2.77 | 1.44 |
| C5 | .0072 | .0130 | .0150 | 1.15 | 2.08 | 1.80 |
| C6 | .0072 | .0156 | .0100 | 0.64 | 1.38 | 2.16 |
| C7 | .0072 | .0182 | .0050 | 0.27 | 0.69 | 2.52 |
| R3 C1 | .0108 | .0026 | .0300 | 11.53 | 2.78 | 0.24 |
| C2 | .0108 | .0052 | .0250 | 4.81 | 2.32 | 0.48 |
| C3 | .0108 | .0078 | .0200 | 2.53 | 1.85 | 0.72 |
| C4 | .0108 | .0104 | .0150 | 1.44 | 1.39 | 0.96 |
| C5 | .0108 | .0130 | .0100 | 0.77 | 0.98 | 1.20 |
| C6 | .0108 | .0156 | .0050 | 0.32 | 0.46 | 1.44 |
| R4 C1 | .0144 | .0026 | .0250 | 9.61 | 1.74 | 0.18 |
| C2 | .0144 | .0052 | .0200 | 3.85 | 1.39 | 0.36 |
| C3 | .0144 | .0078 | .0150 | 1.92 | 1.04 | 0.50 |
| C4 | .0144 | .0104 | .0100 | 0.96 | 0.69 | 0.72 |
| C5 | .0144 | .0130 | .0050 | 0.38 | 0.35 | 0.90 |
| R5 C1 | .0180 | .0026 | .0200 | 7.69 | 1.10 | 0.14 |
| C2 | .0180 | .0052 | .0150 | 2.88 | 0.83 | 0.29 |
| C3 | .0180 | .0078 | .0100 | 1.28 | 0.56 | 0.43 |
| C4 | .0180 | .0104 | .0050 | 0.48 | 0.28 | 0.58 |
| R6 C1 | .0216 | .0026 | .0150 | 5.77 | 0.69 | 0.12 |
| C2 | .0216 | .0052 | .0100 | 1.92 | 0.46 | 0.24 |
| C3 | .0216 | .0078 | .0050 | 0.64 | 0.23 | 0.36 |
| R7 C1 | .0252 | .0026 | .0100 | 3.85 | 0.40 | 0.10 |
| C2 | .0252 | .0052 | .0050 | 0.96 | 0.20 | 0.20 |
| R8 C1 | .0288 | .0026 | .0050 | 1.92 | 0.17 | 0.09 |

¹ These ratio values are based on the supposition that the salts are completely ionized, so that all the Mg, etc., in the solution is regarded as being in the form of Mg, etc., ions. This is, of course, not strictly true, but as the ions are absorbed by the plant more ions should be formed, so that eventually all of these atoms should be available as ions.

A continuous record of the temperature changes during the period of this series was secured by means of a thermograph. The highest temperature recorded was 34° C. (on May 22 and 25) and the lowest was 9° C.

(on May 18 and 20). A cylindrical porous-cup atmometer, which was used to indicate the variations in the evaporating power of the air during the period in question, gave a daily mean water loss of 7.6 c.c., a maximum for a 24-hour period of 13.6 c.c. (on June 5), and a minimum of 1.4 c.c. (on May 30), with a total loss of 182 c.c. for the entire period of 24 days. These readings are all corrected to the Livingston standard cylindrical cup (21) by multiplying the actual readings by the coefficient furnished with the instrument.

In the following sections will be found a discussion of the physiological effects upon the wheat plants, produced by the various solutions, with their different salt-proportions, and a comparison of these results from sand cultures with those obtained by Shive from his corresponding water cultures, and also with Shive's results from his sub-optimal series, in which the total osmotic concentration was 0.1 atmosphere. The behavior of the plants in the different cultures will be compared with reference to the dry weights of tops and of roots and with respect to the relative amounts of water transpired during the growth period.

II. *Dry Weights*

(a) Method Employed in Harvesting

At the end of the growth period the wax seal was removed from the surface of the sand and the contents of the culture pot were carefully transferred to a coarse sieve having approximately 10 meshes to the inch. By means of a gentle stream of water the sand was then washed down through the sieve, leaving the plants and roots behind. The tops of the plants were severed from the roots just above the remnant of the seed and then dried in an electric oven at 80° C. for a period of 24 hours, after which they were dried to constant weight at an oven temperature of approximately 102° C. Since it was impossible to wash the sand entirely free from the roots, a different method of procedure was necessary in order to obtain the dry weight of these subterranean parts. Without attempting to remove the last traces of sand, the roots were transferred from the sieve to a piece of paper and allowed to attain an air-dry condition, after which they were dried in the oven, just as in the case of the tops, until the oven-dry weights were obtained. These included, for each lot of roots, the weight of the adhering sand as well as the weight of the roots themselves. To correct this error the oven-dried roots were ignited in porcelain crucibles until all the organic matter had been destroyed. The loss on ignition of the samples was recorded as representing the approximate dry weight of the roots, upon the assumption that the sand adhering to the roots was all non-combustible and therefore suffered no loss in the ignition process. For practical purposes the small amount of ash resulting from the ignition of the root tissues may be neglected, especially since the relative weights would be affected only by the difference between the weights of the ash from the various individual cultures.

(b) Presentation of Data

In Table VI are presented the transpiration data for the individual cultures, together with the dry weights of tops and of roots. The transpiration data include (1) the actual water loss, in cubic centimeters, of

TABLE VI
TRANSPIRATION RECORD AND DRY WEIGHTS OF TOPS AND OF ROOTS FOR WHEAT GROWN 24 DAYS IN SAND CULTURES, SUPPLIED WITH THREE-SALT SOLUTIONS, ALL HAVING A TOTAL OSMOTIC CONCENTRATION OF 1.75 ATMOSPHERES, BUT DIFFERING FROM EACH OTHER IN THE PROPORTION OF THE THREE SALTS EMPLOYED

| Culture Number | Transpiration (6 Plants) | | Dry Weight of Tops ¹ (6 Plants) | | Dry Weight of Roots ¹ (6 Plants) | |
|----------------|--------------------------|----------------------------|--|----------------------------|---|----------------------------|
| | Total Water Loss | Relative to R1 C1 as Unity | Absolute | Relative to R1 C1 as Unity | Absolute | Relative to R1 C1 as Unity |
| | gm. | | gm. | | gm. | |
| R1 C1 | 175.3 | 1.00 | 0.6412 | 1.00L | .1180 | 1.00L |
| C2 | 245.7 | 1.41 | 0.9504 | 1.48 | .2118 | 1.79 |
| C3 | 273.3 | 1.56 | 1.0723 | 1.67 | .1672 | 1.41L |
| C4 | 271.2 | 1.55 | 1.1276 | 1.75H | .1936 | 1.63L |
| C5 | 316.2 | 1.80 | 1.0612 | 1.65 | .2171 | 1.83 |
| C6 | 321.6 | 1.83 | 1.1882 | 1.85H | .2174 | 1.84 |
| C7 | 341.2 | 1.95 | 1.2181 | 1.90H | .2318 | 1.95 |
| C8 | 339.9 | 1.94 | 1.2811 | 2.00H | .2168 | 1.83 |
| R2 C1 | 205.8 | 1.17 | 0.6285 | 0.95L | .1844 | 1.55L |
| C2 | 248.3 | 1.42 | 0.8474 | 1.32 | .2134 | 1.88 |
| C3 | 303.8 | 1.73 | 1.0445 | 1.68 | .2210 | 1.88 |
| C4 | 353.7 | 2.00 | 1.2770 | 2.00H | .2652 | 2.24H |
| C5 | 339.5 | 1.94 | 1.1428 | 1.78H | .3166 | 2.67H |
| C6 | 321.8 | 1.83 | 1.1420 | 1.78H | .2597 | 2.19 |
| C7 | 391.0 | 2.23^H | 1.4660 | 2.29^H | .3333 | 2.81^H |
| R3 C1 | 236.3 | 1.34 | 0.7080 | 1.11L | .2828 | 2.38H |
| C2 | 306.0 | 1.75 | 1.0358 | 1.62 | .2969 | 2.50H |
| C3 | 263.8 | 1.50 | 0.9072 | 1.43 | .2471 | 2.08 |
| C4 | 312.0 | 1.78 | 1.0140 | 1.58 | .2642 | 2.23H |
| C5 | 314.8 | 1.79 | 1.0810 | 1.71 | .2786 | 2.35H |
| C6 | 336.1 | 1.92 | 1.0972 | 1.73H | .2077 | 1.75 |
| R4 C1 | 192.2 | 1.09 | 0.5201 | 0.86L | .2531 | 2.13 |
| C2 | 308.3 | 1.75 | 1.0330 | 1.62 | .2969 | 2.50H |
| C3 | 260.6 | 1.50 | 0.8310 | 1.30L | .2316 | 1.95 |
| C4 | 327.9 | 1.87 | 1.1033 | 1.72 | .2630 | 2.22 |
| C5 | 302.5 | 1.72 | 0.9848 | 1.54 | .2440 | 2.06 |
| R5 C1 | 237.6 | 1.35 | 0.6822 | 1.07L | .2440 | 2.06 |
| C2 | 251.4 | 1.44 | 0.7790 | 1.23L | .1786 | 1.50L |
| C3 | 251.6 | 1.44 | 0.7763 | 1.21L | .1794 | 1.51L |
| C4 | 289.4 | 1.65 | 0.8912 | 1.39 | .1549 | 1.31L |
| R6 C1 | 261.3 | 1.50 | 0.8489 | 1.32 | .1527 | 1.30L |
| C2 | 306.7 | 1.75 | 0.9151 | 1.43 | .1730 | 1.46L |
| C3 | 358.1 | 2.05 | 0.9460 | 1.48 | .2598 | 2.19 |
| R7 C1 | 208.6 | 1.19 | 0.6285 | 0.95L | .2044 | 1.72 |
| C2 | 286.8 | 1.65 | 0.9540 | 1.50 | .2266 | 1.91 |
| R8 C1 | 277.6 | 1.60 | 0.8466 | 1.32 | .2669 | 2.25H |

¹The best nine cultures are marked H, while the poorest nine are marked L.

each individual culture for the entire growth period and (2) these same quantities expressed as relative to the loss from culture R1 C1, taken as unity. In the dry weight columns are recorded (1) the absolute dry

weights, in grams, of both tops and roots separately and (2) the weights of tops and of roots relative to those of culture R1 C1, taken as unity. The maximum transpiration and the highest yields of tops and roots are here indicated by black-face type. A discussion of the transpiration data will be presented under a separate heading, following the discussion devoted to a comparison of the results obtained in the sand cultures with those secured in solution cultures.

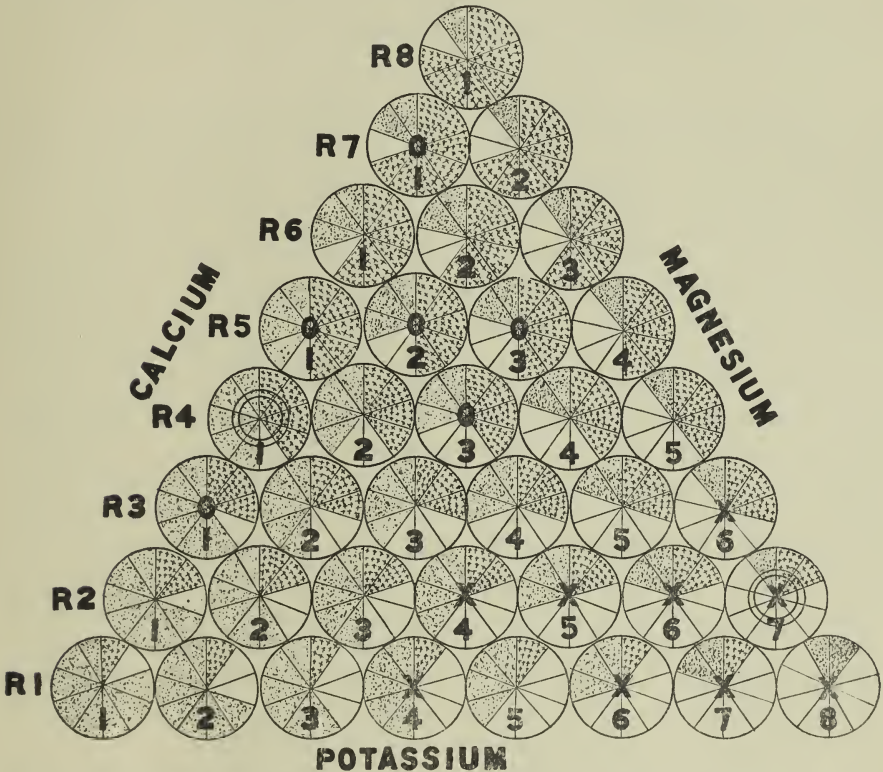


Fig. 2.—Triangular diagram showing the arrangement of the sand cultures with respect to the partial concentrations of the three salts employed. Unshaded segments represent the proportions of $\text{Ca}(\text{NO}_3)_2$: stippled segments the MgSO_4 : and the segments shaded with crosses the KH_2PO_4 . The best nine cultures are marked X, while the poorest nine are marked by O.

In order to study better the relative growth rates, the entire series of 36 cultures are divided into three groups, (1) a lower one-fourth composed of the 9 cultures giving the lowest yields (either tops or roots), (2) an upper one-fourth composed of the 9 cultures giving the highest yield values, and (3) a medium one-half which comprised the remaining cultures. To facilitate the comparison, the solution cultures (38) were treated in exactly the same manner. In Tables VI and VII the relative

yields are marked with an L if they lie in the low yield group and with an H if they lie within the high yield group. The cultures with high and with low values for weights of tops are shown on the diagram of figure 2. These, and similar groups of cultures, are to be found on the diagrams of figures 3 and 5, and will be referred to, always, as the *best* nine and the *poorest* nine.

III. A Comparison of the Results from Sand Cultures with those from Solution Cultures

(a) Dry Weight of Tops

As has been mentioned, the results here brought forward were secured by using seed from the same lot as that from which Shive's seed was selected, and it thus seems desirable to compare the growths secured with these sand cultures with those obtained by Shive with solution cultures.

The second and third columns of Table VII present the relative dry weights of tops and of roots for the various sand cultures here employed, which were all supplied with nutrient solutions of the same total osmotic concentration, but of different salt-proportions, as already described. In columns 4 and 5 of this table are given the relative dry weights of tops and of roots secured by Shive in his sub-optimal cultures, all these solutions having a total osmotic concentration of 0.1 atmosphere. In the two columns at the right of the table are given the relative dry weights of tops and of roots for Shive's optimal series, with solutions having the same total osmotic concentration (1.75 atmospheres) as those employed in the sand cultures of the present study. The *actual* dry weights, in grams, of culture R1 C1 are given in parentheses directly below the relative weight values. The actual dry weight of any culture may be obtained by multiplying the relative weight by the actual weight of culture R1 C1 as given in the same column. Shive's supra-optimal series of cultures, with total concentration of 4.0 atmospheres, is not here considered.

To facilitate a general comparison of these three sets of cultures, the relative yields of tops are graphically shown in the triangular diagrams of figure 3, where A represents the sand cultures and B and C represent Shive's sub-optimum and optimum series, respectively. The areas of high yields are here indicated by crosses and those of low yields are shown by small circles, as was done by Shive. In each diagram the culture giving the highest yield is indicated by a large X.

It is readily apparent that there is a marked similarity, with respect to the location of the area of the poorest growth of tops, between the diagram for the sand cultures (1.75 atmospheres, total concentration, fig. 3, A) and that representing Shive's sub-optimal series (0.1 atmosphere, total concentration, fig 3, B). In fact, all three of the diagrams show a mark-

ed similarity in this respect. The culture giving the highest yield of tops in the sand series is R2 C7, which is characterized by having 2 tenths of

TABLE VII

COMPARISON OF THE RELATIVE DRY WEIGHTS OF TOPS AND OF ROOTS OF WHEAT GROWN IN SAND CULTURES WITH CORRESPONDING DATA FOR WHEAT GROWN IN SOLUTION CULTURES

| Culture Number | Sand Cultures (McCall) Total Concentration of Solution 1.75 atm. | | Sub-optimal and Optimal Solution Cultures (Shive, 1915) | | | |
|--------------------|--|-------------------|--|------------------|----------------------------------|------------------|
| | | | Total Concentration 0.1 atm. | | Total Concentration 1.75 atm. | |
| | Relative Dry Weight ¹ | | Relative Dry Weight | | Relative Dry Weight | |
| | Tops | Roots | Tops | Roots | Tops | Roots |
| R1 C1 | 1.00L (0.6412) | 1.00L (0.1186) | 1.00L (0.2601) | 1.00 (0.1036) | 1.00L (0.4104) | 1.00 (0.1058) |
| C2 | 1.48 | 1.79 | 1.22 | 1.05 | 1.19 | 1.11H |
| C3 | 1.67 | 1.41L | 1.25 | 0.99 | 1.20 | 0.93 |
| C4 | 1.75H | 1.63L | 1.30 | 0.91 | 1.17L | 1.07H |
| C5 | 1.65 | 1.83 | 1.24 | 0.86L | 1.26 | 0.99 |
| C6 | 1.85H | 1.84 | 1.38 | 0.98 | 1.16L | 1.03 |
| C7 | 1.90H | 1.95 | 1.25 | 0.78L | 1.11L | 1.01 |
| C8 | 2.00H | 1.84 | 1.23 | 0.80L | 1.17 | 0.95 |
| R2 C1 | 0.95L | 1.55L | 1.03L | 1.19 | 1.03L | 0.96 |
| C2 | 1.32 | 1.88 | 1.20L | 1.04 | 1.14L | 1.05H |
| C3 | 1.68 | 1.88 | 1.39 | 0.93 | 1.25 | 0.93L |
| C4 | 2.00H | 2.24H | 1.48H | 0.94 | 1.27H | 0.95 |
| C5 | 1.78H | 2.67H | 1.40 | 0.77L | 1.18 | 0.90L |
| C6 | 1.78H | 2.19 | 1.43H | 0.76L | 1.22 | 0.98 |
| C7 | 2.29H | 2.81H | 1.39 | 0.80L | 1.23 | 1.04 |
| R3 C1 | 1.11L | 2.38H | 1.11L | 1.39H | 1.15L | 1.02 |
| C2 | 1.16 | 2.50H | 1.28 | 1.19H | 1.24 | 1.07H |
| C3 | 1.43 | 2.08 | 1.42H | 1.00 | 1.36H | 1.07H |
| C4 | 1.58 | 2.23H | 1.57H | 0.94 | 1.28H | 0.95 |
| C5 | 1.71 | 2.35H | 1.52H | 0.82L | 1.25 | 0.92L |
| C6 | 1.73H | 1.75 | 1.35 | 0.91 | 1.27H | 0.93L |
| R4 C1 | 0.86L | 2.13 | 1.00L | 1.31H | 1.12L | 1.04 |
| C2 | 1.62 | 2.50H | 1.21 | 1.22H | 1.28H | 1.10H |
| C3 | 1.30L | 1.95 | 1.41 | 1.06 | 1.26 | 0.91L |
| C4 | 1.72 | 2.22 | 1.57H | 0.89 | 1.27 | 0.91L |
| C5 | 1.54 | 2.06 | 1.65H | 0.89L | 1.30H | 1.04 |
| R5 C1 | 1.07L | 2.06 | 1.09L | 1.30H | 1.19 | 1.07H |
| C2 | 1.23L | 1.50L | 1.47H | 1.18 | 1.39H | 1.08H |
| C3 | 1.21L | 1.51L | 1.41 | 0.90 | 1.24 | 0.91L |
| C4 | 1.39 | 1.31L | 1.32 | 0.72L | 1.28H | 1.03 |
| R6 C1 | 1.32 | 1.30L | 1.10L | 1.31H | 1.17 | 1.06H |
| C2 | 1.43 | 1.46L | 1.29 | 1.07 | 1.19 | 0.91L |
| C3 | 1.48 | 2.19 | 1.44H | 1.02 | 1.21 | 0.87L |
| R7 C1 | 0.95L | 1.72 | 1.11L | 1.36H | 1.16L | 1.03 |
| C2 | 1.50 | 1.91 | 1.29 | 1.28H | 1.31H | 0.98 |
| R8 C1 | 1.32 | 2.25H | 1.10L | 1.35H | | |
| Check ² | 0.52 | 1.78 | | | | |

¹ The dry weight of culture R1 C1 is always taken as unity and the other weights are expressed in terms of this value. The actual dry weight of culture R1 C1 is given in parentheses, in grams. The best nine cultures are marked H, while the poorest are marked L.

² Check received only distilled water.

its total osmotic concentration derived from mono-potassium phosphate, 7 tenths from calcium nitrate and 1 tenth from magnesium sulphate. This

culture gave a yield of dry tops 129 per cent greater than that of R1 C1. The culture giving the highest yield of tops in Shive's sub-optimal solution cultures was R4 C5, its yield being 65 per cent higher than that from culture R1 C1 in the same series. This culture solution is characterized

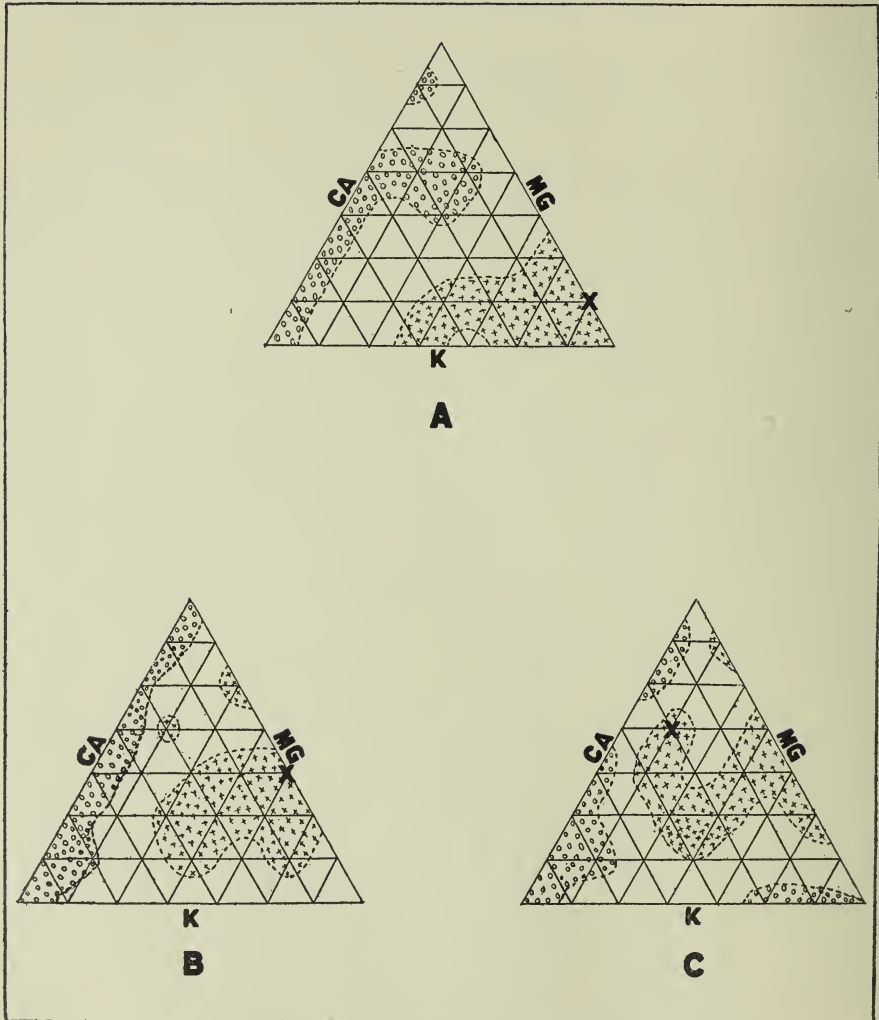


Fig. 3.—Triangular diagrams showing areas of high and of low yield of tops. A, sand cultures; B, Shive's sub-optimal, and C, Shive's optimal solution cultures.

by having 4 tenths of its total osmotic concentration derived from monopotassium phosphate, 5 tenths from calcium nitrate and 1 tenth from magnesium sulphate. In Shive's optimal series (1.75 atmospheres) the highest dry weight of tops was obtained from culture R5 C2, and this

yield was 39 per cent higher than that from culture R1 C1 in the same series. This solution is characterized by having 5 tenths of its total osmotic concentration due to mono-potassium phosphate, 2 tenths to calcium nitrate, and 3 tenths to magnesium sulphate. These data are summarized in Table VIII.

TABLE VIII

OSMOTIC PROPORTIONS OF THE THREE-SALT SOLUTIONS GIVING THE BEST GROWTH OF TOPS IN THE SAND CULTURE SERIES (McCALL) AND IN THE SUB-OPTIMAL AND OPTIMAL SOLUTION SERIES (SHIVE)

| Series | Relative Dry Weight of Tops | Total Concentration atm. | Osmotic Proportions, in Tenths, of of Total Concentration | | |
|------------------------|-----------------------------|--------------------------|---|-----------------------------------|-------------------|
| | | | KH ₂ PO ₄ | Ca(NO ₃) ₂ | MgSO ₄ |
| Sand Cultures (McCall) | 2.29 | 1.75 | 2 | 7 | 1 |
| Sub-optimal (Shive) .. | 1.65 | 0.10 | 4 | 5 | 1 |
| Optimal (Shive) | 1.39 | 1.75 | 5 | 2 | 3 |

A comparison of the best sand culture (total concentration 1.75 atmospheres) with the best solution culture of the sub-optimal series (total concentration 0.1 of an atmosphere) brings out the fact that the osmotic concentration ratio of magnesium sulphate to mono-potassium phosphate plus calcium nitrate is the same for both cultures, namely 1:9. The ratio of magnesium sulphate to calcium nitrate is 1:7 for the sand culture and 1:5 for the solution culture. The greatest difference between the relative proportions of the salts employed is shown by the ratio of calcium nitrate to mono-potassium phosphate, this ratio being 7:2 for the sand and 5:4 for the solution culture.

A comparison of the best sand culture with the solution culture giving the best growth of tops in Shive's optimal series, having the same total osmotic concentration (1.75 atm.) brings out some surprising results. In these two cultures there is a marked difference in salt proportions. Shive's best solution in his optimal series is characterized by a value of 3:7 for the osmotic ratio of magnesium sulphate to calcium nitrate plus mono-potassium phosphate; while in the best culture of the sand series and the best in the sub-optimal solution series this ratio is 1:9, as has already been stated. The most striking difference between the best culture of the sand series and the best of Shive's optimal water-culture series is found, however, in the relation of magnesium to calcium. In the best solution of Shive's series the osmotic ratio of magnesium sulphate to calcium nitrate is 3:2, while for the best culture of the sand series this ratio is 1:7. The osmotic ratio of the calcium salt to the potassium salt is also markedly different in these two cases, being 2:5 for the best solution culture and 7:2 for the best sand culture.

While it appears to be impossible to draw any definite conclusions from a detailed study of the characteristics of the solutions that produced

the best growth of tops in the three series it is important to note (1) that the results secured in the sub-optimal solution series are more nearly like those from the sand series than are the results obtained from the optimal solution series with the same total osmotic concentration; (2) that there is a marked difference between the solutions producing the best growth of tops in sand and those giving the best growth of tops in solution cultures, with respect to the osmotic proportions of the three salts employed. Attention is called to the fact that the improvement in growth of tops as we proceed to the right from the left margin of the triangle is very much more marked in the sand than in the solution series. This is brought out in a striking manner by the graphs of figure 4, which show the variations in the yield of tops of the individual cultures in the sand series and in Shive's optimal and sub-optimal solution series.

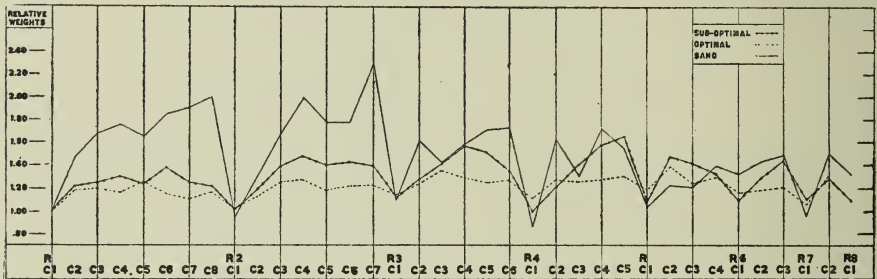


Fig. 4.—Relative dry weights of cultures grown in sand and in solution cultures of sub-optimal and of optimal total concentrations.

The most striking feature of these graphs is the regularity with which the one for the sand series of cultures intersects those for the two solution series. It will be seen that this intersection occurs always at culture No. 1 of each row, as represented on the triangular diagram, with the exception of R6 C1 and of R8 C1. A possible explanation of the phenomenon thus indicated is offered by the known selective adsorptive property of sand and other finely divided substances.

As early as 1866, Frank (11), studied the retention of potassium chloride by the soil, finding that soil has the power of absorbing, or removing from solution, considerable amounts of this salt. Subsequent investigations have shown that this power to remove salts from solution is also possessed by other finely divided substances that are chemically inert, such as charcoal and pulverized silica. More recent work has not only confirmed these early observations, but has brought out the fact that finely divided substances may exercise a selective action with respect to the solution with which they are brought into contact. In some cases the effect of this selective

action is to remove one ion of the salt more rapidly than the other, leaving the solution alkaline or acid, depending upon which ion is removed to the greater extent.¹ It has also been found that, in certain cases, the selective adsorption increases in amount with the concentration of the solution, up to a certain maximum, and then remains constant with still further increase in concentration.

To employ these considerations in an attempt to explain the physiological phenomena in question, it may be supposed that the poor growth of all of the C1 cultures, whether in sand or solution, is due to a deficiency of calcium nitrate together with the accompanying excess of magnesium sulphate, thus leaving out of account, for the present, row 6 and the single culture at the apex of the diagram. In the solution cultures, as we pass from C1 to C2, in each row, the proportion of calcium nitrate to magnesium sulphate becomes slightly more favorable, giving rise to a slight increase in the dry weight from C2 as compared with C1. It may also be supposed that the partial concentration of the magnesium salt is here the factor limiting the growth of the plants and that this salt antagonizes the NO_3 radical, thus preventing the latter from exerting an accelerating influence on the growth rate. In the sand cultures it is possible that the NO_3 radical is not appreciably adsorbed by the sand, but that a part of the magnesium present in the system is so adsorbed, thus being prevented from active participation in the physiological processes of the plants.²

To go farther with this hypothesis, it may be supposed that this adsorption of magnesium is not sufficient, in the left cultures of the diagram, to allow the NO_3 ions to assert themselves by accelerating the growth of the plants. As we proceed toward the right, on the triangular diagram, the partial concentration of magnesium sulphate in the original solution decreases by increments of 1 tenth of the total concentration, from each culture to the next. Now, the magnesium sulphate actually free to affect the plants of the sand cultures is the amount of this salt in the original solution minus the amount that has been adsorbed by the sand, and it may thus be that the very marked progressive improvement in growth as we proceed from left to right across the diagram is due to a parallel increase in the partial concentration of the calcium nitrate accompanied by a corresponding decrease in the magnesium sulphate. This alteration in the salt-proportions (or ion-proportions) of the unadsorbed solution brought about by the selective adsorption of magnesium sulphate by the solid medium, may give rise to a better physiological balance than that which characterizes the unmodified solution.

¹ See in this connection: Gore, G. (12); Briggs, J. L. (3); Cameron, F. C., and Bell, J. M. (6); Parker, E. G. (29); Williams, A. M. (45); and McCall, A. G. (26).

² While no direct evidence bearing upon this point can be produced, it may be mentioned that Parker (29, p. 188) found that sodium nitrate in certain partial concentrations increased the adsorption, by the soil, of potassium chloride out of the same solution.

(b) Dry Weight of Roots

The dry weights of roots are given in Table VII, in connection with the dry weights of tops. The graph presented in figure 6 shows the variation in dry weight of roots between the individual cultures. The marked characteristic of this diagram is the manner in which the graph makes a gradual rise to near the middle of the series and then gradually declines until near the end, where a slight rise again occurs.

The discussion of these data can best be presented by referring to the triangular diagram of figure 5A, in which the area of high relative values is indicated by crosses and that of low values is marked by circles. The relative dry weights of roots have a total range from 1.00 (culture R1 C1) to a maximum of 2.81 (culture R2 C7). A comparison of this diagram with figure 3A, giving the dry weights of tops, brings out the interesting fact that the culture showing the best growth of roots (culture R2 C7) is also the one that gave the highest yield of tops. This culture gave 129 per cent greater yield of tops and 181 per cent greater yield of roots than did culture R1 C1. No such correlation is apparent, however, between the culture giving the poorest yield of tops and the one showing the poorest root development.

Considering, now, the areas of high and of low root yields, it will be seen that an area of high yields (2.22 to 2.81) extends nearly across the entire width of the triangle, in a regular belt beginning at row 2 on the right and passing obliquely upward to the center of the triangle (where a slight break occurs) thence to the right margin at row 3. In a similar manner an area of low yields (1.30 to 1.51) extends across the entire width of the triangle, occupying a position above the area of high yields and being confined to rows 5 and 6. Two small areas of low yields are shown at the lower margin of the diagram, each of which includes two cultures.

The solution giving the best growth of roots, as in the case of tops, is characterized by having 2 tenths of its total osmotic concentration derived from mono-potassium phosphate, 7 tenths from calcium nitrate and the remaining 1 tenth from magnesium sulphate.

The culture giving the poorest growth of roots is culture R1 C1, which lies outside of the main area of low root yields. This culture has 1 tenth of its total osmotic concentration due to mono-potassium phosphate, 1 tenth to calcium nitrate, and the remaining 8 tenths to magnesium sulphate.

A comparison of this diagram with the corresponding diagrams (figure 5, B and C) of Shive's solution cultures serves to bring out the fact that the areas of highest and of lowest yields of roots extend in narrow strips across the triangular diagram for the sand cultures in a direction almost at right angles to the direction taken by the corresponding areas on the diagrams representing the solution cultures with total concentra-

tion of 0.1 and 1.75 atmospheres. A comparison of the root yields obtained from the sand cultures with those obtained from the solutions of the same total concentration as was used in the sand series (1.75 atm.) and also with those obtained from solutions having a concentration of 0.1 atmosphere fails to reveal any further generalization that might be of interest or value in this connection.

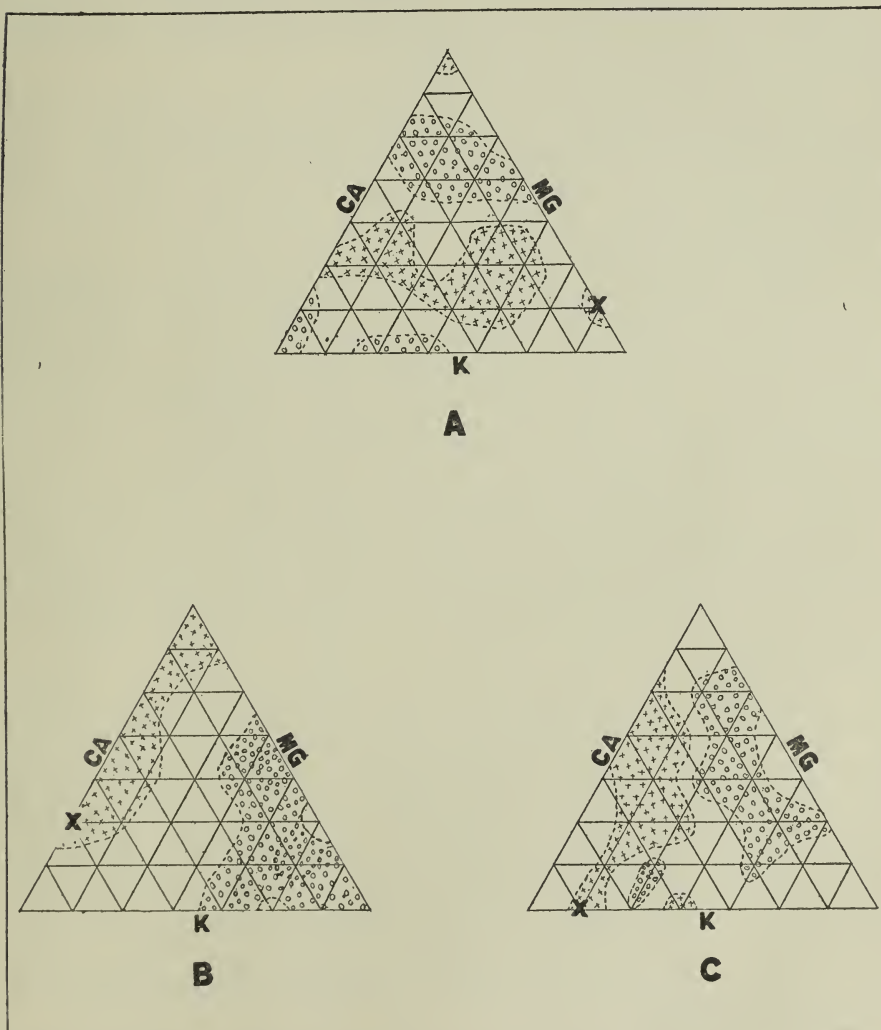


Fig. 5.—Triangular diagram showing areas of high and of low yield of roots. A, sand cultures; B, Shive's sub-optimal, and C, Shive's optimal solution cultures.

IV. Relation of Top Yields to Cation Ratio Values

Introduction. The dissociation of the three salts employed in these culture solutions gives rise to three kinds of cations (Ca, K and Mg) and three kinds of anions (NO_3 , PO_4 and SO_4), if we assume a com-

plete ionization of the salts and disregard the H ions and the HPO_4 ions produced by the dissociation of mono-potassium phosphate. Since these chemical units also appear to function as units in the metabolic processes of the plant, and since absorption of any ion by the plant should lead to further production of that ion in the solution, until all of the molecules in question, originally present, had been separated into ions, it is of interest to study the relation between the ion ratios and the yield of tops, somewhat as was done by Shive in his study of solution cultures corresponding to the sand cultures here considered.

As the last mentioned writer has pointed out, one of these three-salt solutions may be defined by the three cation ratios, Mg/Ca, Mg/K and Ca/K, for the values of any other of the possible ion ratios may be found directly from these three. The cation ratio values alone will therefore be considered in this discussion.

It should be noted at once that the ionic ratios may be very greatly modified by the presence of the sand, which, through its adsorptive power may not only markedly reduce total concentration of the original solution, but may also alter the original relative proportions of the component salts and ions. As has been emphasized above, the adsorptive action may fall more heavily on some of the ions than upon others, so that the unadsorbed solution remaining in the sand of the culture pots may be characterized by very different molecular and ionic ratios from those of the original solutions with which the pots were first saturated. It is highly probable that selective adsorption plays an important rôle in bringing about the physiological differences to be observed between the sand cultures of the present paper and the corresponding solution cultures of Shive's study.

Dry weight of tops. Range of cation ratios for the best nine cultures. Table IX presents the cation ratio values for each of the nine solutions (of the sand cultures and of the sub-optimal and optimal) that produced the highest yield of tops. The best nine cultures, in each case, are the ones marked H in Tables VI and VII. The cultures are here (Table IX) arranged in the descending order, on the basis of top yields, the one producing the highest yield in each series being placed at the head of the column. In the columns giving the cation ratios the minimum and the maximum values for these ratios are marked L and H, respectively. The total range in the magnitude of these ratio values is given at the bottom of the respective column.

It will be observed that the group of sand-culture solutions giving high yields of tops is characterized by a comparatively low range (2.16) in the Mg/Ca ratio value, extending from minimum of 0.24 to maximum of 2.40. This group of highest yielding cultures includes the lowest value of this ratio, but is restricted to the lower one-sixth of the total range of these ratio values. Both the Mg/K and the Ca/K ratio values show a

much larger range than does the Mg/Ca ratio. From a consideration of these data it may be concluded that in sand cultures, such as were here employed, we may expect to find good growth of tops associated with Mg/Ca ratio values between 0.24 and 2.40; a range of Mg/K ratio values from 0.46 to 6.94; and a range of Ca/K ratio values from 1.44 to 5.77. The culture (R2 C7) giving the largest yield of tops is characterized by a low Mg/Ca ratio (0.46), a low Mg/K ratio value (0.69) and an intermediate value (2.52) for the Ca/K ratio.

TABLE IX

RANGE OF CATION RATIO VALUES AND RELATIVE DRY WEIGHTS OF TOPS OF THE BEST NINE CULTURES OF WHEAT GROWN IN SAND AND IN SOLUTION CULTURES

| | Culture Numbers | Cation Ratio Values | | | Yield of Tops Relative to that of Culture R1 C1 |
|--|-----------------|---------------------|-------------------|-------------------|---|
| | | Mg/Ca | Mg/K | Ca/K | |
| Sand cultures supplied with a solution having a concentration of 1.75 atm. | R2 C7 | 0.27 | 0.69 | 2.52 | 2.29 |
| | R1 C8 | 0.24 _L | 1.39 | 5.77 _H | 2.00 |
| | R2 C4 | 1.92 | 2.77 | 1.44 | 2.00 |
| | R1 C7 | 0.55 | 2.78 | 5.04 | 1.90 |
| | R1 C6 | 0.96 | 4.17 | 4.33 | 1.85 |
| | R2 C5 | 1.15 | 2.05 | 1.80 | 1.78 |
| | R2 C6 | 0.64 | 1.38 | 2.16 | 1.78 |
| | R1 C4 | 2.40 _H | 6.94 _H | 2.88 | 1.75 |
| | R3 C5 | 0.32 | 0.46 _L | 1.44 _L | 1.73 |
| Range | | 2.16 | 6.48 | 4.33 | |
| Solution cultures of sub-optimal concentration 0.1 atm. (Shive) | R4 C5 | 0.38 _L | 0.35 | 0.90 | 1.65 |
| | R3 C4 | 1.44 | 1.39 | 0.96 | 1.57 |
| | R4 C4 | 0.96 | 0.69 | 0.72 | 1.57 |
| | R3 C5 | 0.77 | 0.93 | 1.20 | 1.52 |
| | R2 C4 | 1.92 | 2.77 _H | 1.44 | 1.48 |
| | R5 C2 | 2.88 _H | 0.83 | 0.29 _L | 1.47 |
| | R6 C3 | 0.64 | 0.23 _L | 0.36 | 1.44 |
| | R2 C6 | 0.64 | 1.39 | 2.16 _H | 1.43 |
| | R3 C3 | 2.56 | 1.85 | 0.72 | 1.42 |
| Range | | 2.50 | 2.54 | 1.87 | |
| Solution cultures of optimal concentration 1.75 atm. (Shive) | R5 C2 | 2.88 | 0.83 | 0.29 | 1.39 |
| | R3 C3 | 2.56 | 1.85 | 0.72 | 1.36 |
| | R7 C2 | 0.96 | 0.20 _L | 0.20 _L | 1.31 |
| | R4 C5 | 0.33 | 0.35 | 0.90 | 1.30 |
| | R4 C2 | 3.85 _H | 1.39 | 0.36 | 1.28 |
| | R5 C4 | 0.48 | 0.28 | 0.58 | 1.28 |
| | R3 C4 | 1.44 | 1.39 | 0.96 | 1.28 |
| | R3 C6 | 0.32 _L | 0.46 | 1.44 | 1.27 |
| | R2 C4 | 1.92 | 2.77 _H | 1.44 _H | 1.27 |
| Range | | 3.53 | 2.57 | 1.24 | |

From a comparison of these ratio values with those obtained in the solution cultures, it will be seen that, with respect to the Mg/Ca ratio, there is substantial agreement, the range for the sand culture series being 2.16, that for Shive's solution culture series, with total osmotic concentration of 0.1 atm., 2.50, and for the solution cultures, with a total osmotic

concentration of 1.75 atm., the range is 3.53. The range of the Mg/K ratio value is much greater for the sand culture series than for the solution culture series, both of which are characterized by a medium low range for this ratio. The range of the Ca/K ratio value for the sand cultures is very wide, and includes all possible values except a few of the very lowest. The solution culture series, on the contrary, show low ranges of this ratio and include neither the high nor any of the extremely low ratio values.

From these data it appears that there is substantial agreement between the three series with respect to the range of the Mg/Ca ratio of the solutions employed, but that no such agreement is to be found with respect to the other two cation ratios here considered, hence we may conclude that for the three-salt solution here employed the ratio of magnesium to calcium is more important than the ratio of magnesium to potassium or of calcium to potassium, in determining the best yield of tops. Attention is here directed to the fact that the first mentioned ratio is very closely related to the lime-magnesia ratio, so much discussed, and for this reason it will receive attention in a special chapter.

Dry weight of tops. Range of cation ratios for the poorest nine cultures. Table X shows the cation ratio values for each of the nine solutions (both sand and solution culture series) that produced the lowest yield of tops. The poorest nine cultures, in each case, are the ones marked L in Tables VI and VII. The cultures are here (Table X) arranged in the ascending order, the one producing the lowest yield in each series being placed at the head of the column. As in the previous section (Table IX), the minimum and the maximum values for the ratios are marked L and H, and the total range in the magnitude of these ratio values is given at the bottom of the respective column.

It will be observed that the group of sand-culture solutions giving the lowest yield of tops is characterized by a very wide range in the Mg/Ca ratio values, which include all but the very lowest values. The Mg/K ratios cover practically the entire range of values, while the Ca/K ratio shows a very low range, which is confined to the low values. The poorest individual culture is characterized by a high (9.61) Mg/Ca ratio, a low (1.74) Mg/K ratio, and a very low (0.18) Ca/K ratio. From a consideration of these data, it may be concluded, that in sand cultures such as were here employed, we may expect to find poor growth of tops associated with a very low ratio of calcium to potassium. It appears, further, that the ratios of magnesium to potassium and of calcium to potassium are not important factors in bringing about a *poor* growth of tops.

From a comparison of these ratio values with those obtained in the solution cultures it will be seen that with respect to the range in the Mg/Ca and the Mg/K ratio values there is a very close agreement, the range being very wide for all three of the series here considered. With

respect to the range in the Ca/K ratios there is perfect agreement between the sand culture series (1.75 atm.) and the sub-optimal (0.1 atm.) solution culture series, the range in both cases being very narrow, but the optimal (1.75 atm.) solution culture series has a wide range for this ratio.

TABLE X

RANGE OF CATION RATIO VALUES AND RELATIVE DRY WEIGHTS OF TOPS OF THE POOREST NINE CULTURES OF WHEAT GROWN IN SAND AND IN SOLUTION CULTURES

| | Culture Numbers | Cation Ratio Values | | | Yield of Tops Relative to that of Culture R1 C1 |
|--|-----------------|---------------------|--------------------|-------------------|---|
| | | Mg/Ca | Mg/K | Ca/K | |
| Sand cultures supplied with a solution having a concentration of 1.75 atm. | R4 C1 | 9.61 | 1.74 | 0.18 | 0.86 |
| | R2 C1 | 13.46 | 4.86 | 0.36 | 0.95 |
| | R7 C1 | 3.85 | 0.40 _L | 0.10 _L | 0.95 |
| | R1 C1 | 15.40 _H | 11.10 | 0.72 _H | 1.00 |
| | R5 C1 | 7.69 | 11.11 _H | 0.14 | 1.07 |
| | R3 C1 | 11.53 | 2.78 | 0.24 | 1.11 |
| | R5 C3 | 1.28 _L | 0.56 | 0.43 | 1.21 |
| | R5 C2 | 2.88 | 0.83 | 0.29 | 1.23 |
| | R4 C3 | 1.92 | 1.04 | 0.54 | 1.30 |
| | Range | | 14.12 | 10.70 | 0.62 |
| Solution cultures of sub-optimal concentration 0.1 atm. (Shive) | R1 C1 | 15.40 _H | 11.10 _H | 0.72 _H | 1.00 |
| | R4 C1 | 9.61 | 1.74 | 0.13 | 1.00 |
| | R2 C1 | 13.46 | 4.86 | 0.36 | 1.03 |
| | R5 C1 | 7.70 | 1.11 | 0.14 | 1.09 |
| | R6 C1 | 5.77 | 0.69 | 0.12 | 1.10 |
| | R8 C1 | 1.92 _L | 0.18 _L | 0.10 _L | 1.10 |
| | R3 C1 | 11.55 | 2.78 | 0.24 | 1.11 |
| | R7 C1 | 3.85 | 0.40 | 0.10 | 1.11 |
| | R2 C2 | 5.77 | 4.17 | 0.72 | 1.20 |
| | Range | | 13.48 | 10.92 | 0.62 |
| Solution cultures of optimal concentration 1.75 atm. (Shive) | R1 C1 | 15.40 _H | 11.10 _H | 0.72 | 1.00 |
| | R2 C1 | 13.46 | 4.86 | 0.36 | 1.03 |
| | R1 C7 | 0.55 | 2.78 | 5.04 _H | 1.11 |
| | R4 C1 | 9.61 | 1.74 | 0.18 | 1.12 |
| | R2 C2 | 5.77 | 4.17 | 0.72 | 1.14 |
| | R3 C1 | 11.55 | 2.78 | 0.24 | 1.15 |
| | R1 C6 | 0.96 _L | 4.17 | 4.32 | 1.16 |
| | R7 C1 | 3.85 | 0.40 _L | 0.10 _L | 1.16 |
| | R1 C4 | 2.40 | 6.96 | 2.88 | 1.17 |
| | Range | | 14.44 | 10.70 | 4.94 |

Dry weight of roots. Range of cation ratios for the best nine cultures. In Table XI are presented the cation ratio values for the best nine cultures (both sand and solution culture series) based on the dry weight of roots. As in case of the dry weight of tops, the best nine cultures in every case are the ones marked H in Tables VI and VII, the order of arrangement and the numbering of the high and low ratio values being the same as that followed in Table IX. It will be seen that the group of

sand culture solutions giving high yield of roots is characterized by a very wide range (11.26) for the Mg/Ca ratio values and medium low ranges (2.60 and 2.43, respectively) for the Mg/K and Ca/K ratios. The individual culture giving the largest weight of roots is characterized by very low values for both the Mg/Ca and the Mg/K cation ratios, and a medium value for the Ca/K ratio. The ratio ranges of the sand culture series

TABLE XI
RANGE OF CATION RATIO VALUES AND RELATIVE DRY WEIGHTS OF ROOTS OF THE BEST NINE CULTURES OF WHEAT GROWN IN SAND AND IN SOLUTION CULTURES

| | Culture Numbers | Cation Ratio Values | | | Yield of Roots Relative to that of Culture R1 C1 |
|--|-----------------|---------------------|-------------------|-------------------|--|
| | | Mg/Ca | Mg/K | Ca/K | |
| Sand cultures supplied with a solution having a concentration of 1.75 atm. | R2 C7 | 0.27 _L | 0.69 | 2.52 _H | 2.81 |
| | R2 C5 | 1.15 | 2.08 | 1.80 | 2.67 |
| | R4 C2 | 3.85 | 1.39 | 0.36 | 2.50 |
| | R3 C2 | 4.81 | 2.32 | 0.48 | 2.50 |
| | R3 C1 | 11.53 _H | 2.73 _H | 0.24 | 2.38 |
| | R3 C5 | 0.77 | 0.93 | 1.20 | 2.35 |
| | R8 C1 | 1.92 | 0.18 _L | 0.09 _L | 2.25 |
| | R2 C4 | 1.92 | 2.77 | 1.44 | 2.24 |
| | R3 C4 | 1.44 | 1.39 | 0.96 | 2.23 |
| Range | | 11.26 | 2.60 | 2.43 | |
| Solution cultures of sub-optimal concentration 0.1 atm. (Shive) | R3 C1 | 11.55 _H | 2.78 _H | 0.24 | 1.39 |
| | R7 C1 | 3.85 | 0.40 | 0.10 | 1.36 |
| | R8 C1 | 1.92 | 0.18 _L | 0.09 _L | 1.35 |
| | R4 C1 | 9.61 | 1.74 | 0.18 | 1.31 |
| | R6 C1 | 5.77 | 0.69 | 0.12 | 1.31 |
| | R5 C1 | 7.70 | 1.11 | 0.14 | 1.30 |
| | R7 C2 | 0.96 _L | 0.20 | 0.20 | 1.28 |
| | R4 C2 | 3.85 | 1.39 | 0.36 | 1.22 |
| | R3 C2 | 4.81 | 2.32 | 0.48 _H | 1.19 |
| Range | | 10.59 | 2.60 | 0.39 | |
| Solution cultures of optimal concentration 1.75 atm. (Shive) | R1 C2 | 6.74 | 9.72 _H | 1.44 | 1.11 |
| | R4 C2 | 3.85 | 1.39 | 0.36 | 1.10 |
| | R5 C2 | 2.88 | 0.83 | 0.29 | 1.08 |
| | R3 C2 | 4.81 | 2.32 | 0.48 | 1.07 |
| | R1 C4 | 2.40 _L | 6.95 | 2.88 _H | 1.07 |
| | R5 C1 | 7.70 _H | 1.11 | 0.14 | 1.07 |
| | R3 C3 | 2.56 | 1.85 | 0.72 | 1.07 |
| | R6 C1 | 5.77 | 0.69 _L | 0.12 _L | 1.06 |
| | R2 C2 | 5.77 | 4.17 | 0.72 | 1.05 |
| Range | | 5.30 | 9.03 | 2.76 | |

show a substantial agreement with those of the solution culture series of sub-optimal (0.1 atm.) concentration with respect to the range in the Mg/Ca and Mg/K ratios, and a close agreement with the optimal solution (1.75 atm.) series with respect to the range in the Ca/K ratios. As was the case when groups of best cultures of the three series were compared on the basis of dry weight of tops, there is a much closer agreement with respect to the range in value of the Mg/Ca ratio than for the range

of Mg/K and Ca/K ratios. It appears, further, that the contact of the solution with the sand has not markedly changed the correspondence between the range of the Mg/Ca ratio and yield of tops and of roots.

Attention is called to the fact that the groups of best cultures on the basis of dry weight of tops were characterized throughout the three series by a comparatively narrow range in the value of the Mg/Ca ratio, while

TABLE XII

RANGE OF CATION RATIO VALUES AND RELATIVE DRY WEIGHTS OF ROOTS FOR THE POOREST NINE CULTURES OF WHEAT GROWN IN SAND AND IN SOLUTION CULTURES

| | Culture Numbers | Cation Ratio Values | | | Yield of Roots Relative to that of Culture R1 C1 |
|--|-----------------|---------------------|--------------------|-------------------|--|
| | | Mg/Ca | Mg/K | Ca/K | |
| Sand cultures supplied with a solution having a concentration of 1.75 atm. | R1 C1 | 15.40 ^H | 11.10 ^H | 0.72 | 1.00 |
| | R6 C1 | 0.48 ^L | 0.28 ^L | 0.58 | 1.30 |
| | R5 C4 | 5.77 | 0.69 | 0.12 ^L | 1.31 |
| | R1 C3 | 3.85 | 8.34 | 2.16 | 1.41 |
| | R6 C2 | 1.92 | 0.46 | 0.24 | 1.46 |
| | R5 C2 | 2.88 | 0.83 | 0.29 | 1.50 |
| | R5 C3 | 1.28 | 0.56 | 0.43 | 1.51 |
| | R2 C1 | 13.46 | 4.86 | 0.36 | 1.55 |
| | R1 C4 | 2.40 | 6.94 | 2.88 ^H | 1.63 |
| Range | | 14.92 | 10.82 | 2.76 | |
| Solution cultures of sub-optimal concentration 0.1 atm. (Shive) | R5 C4 | 0.48 | 0.28 ^L | 0.58 ^L | 0.72 |
| | R2 C6 | 0.64 | 1.29 | 2.16 | 0.76 |
| | R2 C5 | 1.15 | 2.08 | 1.80 | 0.77 |
| | R1 C7 | 0.55 | 2.78 | 5.04 | 0.78 |
| | R2 C7 | 0.27 | 0.69 | 2.52 | 0.80 |
| | R1 C8 | 0.24 ^L | 1.39 | 5.76 ^H | 0.80 |
| | R3 C5 | 0.77 | 0.93 | 1.20 | 0.82 |
| | R1 C5 | 1.54 ^H | 5.55 ^H | 3.60 | 0.86 |
| | R4 C5 | 0.38 | 0.35 | 0.90 | 0.89 |
| Range | | 1.30 | 5.27 | 5.18 | |
| Solution cultures of optimal concentration 1.75 atm. (Shive) | R6 C3 | 0.64 | 0.23 ^L | 0.36 ^L | 0.87 |
| | R2 C5 | 1.15 | 2.08 | 1.80 ^H | 0.90 |
| | R4 C3 | 1.92 | 1.04 | 0.54 | 0.91 |
| | R4 C4 | 0.96 | 0.69 | 0.72 | 0.91 |
| | R5 C3 | 1.28 | 0.56 | 0.43 | 0.91 |
| | R6 C2 | 1.92 | 0.46 | 0.24 | 0.91 |
| | R3 C5 | 0.77 | 0.93 | 1.20 | 0.92 |
| | R3 C6 | 0.32 ^L | 0.46 | 1.44 | 0.93 |
| | R2 C3 | 3.21 ^H | 3.47 ^H | 1.08 | 0.93 |
| Range | | 2.89 | 3.24 | 1.44 | |

the groups of best cultures on the dry weight of *roots* are characterized by a wide range in the same ratio.

Dry weight of roots. Range of cation ratios for the poorest nine cultures. Table XII shows the cation ratio values and their range for each series, the arrangement of the data being the same as that of the three tables directly preceding. The group of sand cultures shows a very wide

range in the Ca/K ratios. The individual culture showing the poorest growth is characterized by a very high (15.40) Mg/Ca ratio, a very high (11.10) Mg/K ratio, and a low (0.72) Ca/K ratio value. A comparison of the sand and the solution cultures fails to bring out any correlation with respect to the ranges in the cation ratio values as set forth in this table.

V. Water-Requirements

(a) Transpiration Data

Throughout the entire growth period of these cultures the pots were weighed, and the transpiration loss was recorded, at the end of each 3-day interval. The total water loss for each culture was then determined by summing the losses thus recorded for the entire period. The transpiration data for the entire series has been presented in Table VI in connection with the dry weights of tops and roots. In that table the water-losses have been expressed in terms of the loss from culture R1 C1. To bring out the close agreement between the relative water-loss and dry weight of tops, these data have been plotted as shown in the graphs presented in

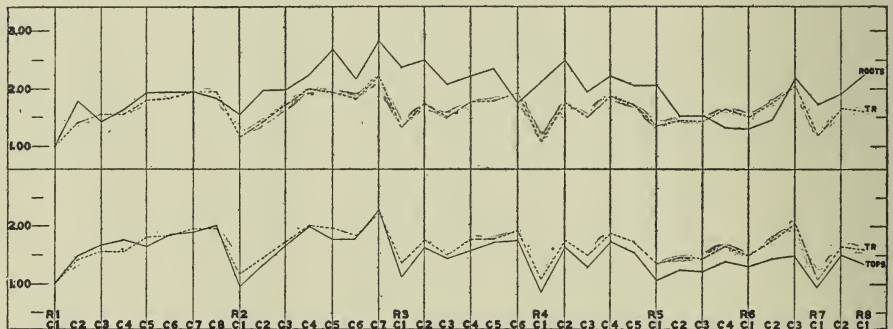


Fig. 6.—Relative transpiration and dry weight of tops and of roots of wheat grown in sand cultures for a period of 24 days.

figure 6. The abscissas are taken to represent the different cultures and the ordinates to indicate the relative dry weights and the transpiration losses relative to the loss from R1 C1 taken as unity. The broken line represents the variation in the relative dry weights of the individual cultures, while the solid line shows the variation in the water-loss from the same cultures.

The data presented in Table VI, and shown by the graphs of figure 6, appear to support the conclusion of Whitney and Cameron (44) and of other workers (20, 22) in the United States Bureau of Soils, to the effect that the total transpirational loss from a plant culture is approximately proportional to the growth made by the plants during the period of time considered. However, as has been pointed out by Livingston (19), this

generalization may be considered as approximately true only for plants of the same species and of the same age, grown with the same aerial environment but in different solutions. This writer concludes that, under the conditions of his experiments the amount of water lost by transpiration is roughly proportional to the extent of the leaf surface of the plant, which, in turn, is related to the size and, therefore, roughly, to the dry weight. Shive (38, p. 375) has emphasized the point that this relation can hold only where the transpiration loss is determined almost entirely by the size of the plant (area of its surface), and not by internal physiological conditions.

(b) Water-Requirement per Gram of Dry Tops

Introductory considerations. The ratio between the amount of water lost by transpiration during a period, and the dry weight of plants produced in the same time, is a convenient term by which to express the water requirements of the plants, since such a ratio is the quantitative expression of the number of grams of transpirational water required to produce a single gram of dry substance.

An excellent review of the early literature upon this subject has been published recently by the United States Department of Agriculture (5) and need not be reviewed in this paper. However, attention should be called to the fact that the results obtained by Sorauer and by Heinrich in controlled solution cultures are in agreement with the recent work of Shive (38, p. 378) with respect to the effect of the total concentration upon the water-requirements of the plants. The results brought forward by these investigators appear to lead to the general conclusion that the higher the total concentration of the nutrient medium, the lower is the ratio between the amount of water transpired and the dry yield of the plants. However, this generalization can hold only within a certain range of concentrations, since it is obvious that as the concentration is increased a point must be reached finally where no growth is possible. The present sand culture series offers an opportunity to study the variation in the water-requirements of these wheat plants when grown in solutions of the same total concentration (approximately optimal), but with a wide variation in the relative partial concentrations of the three salts employed.

Presentation of data. In columns 2, 3 and 4 of Table XIII the absolute transpiration ratios for tops, for roots, and for the entire plant, including both tops and roots, are given. These values were obtained by dividing the total water-loss from the individual cultures by the corresponding dry weight yields. In the last column of the table are also presented the ratios of top yield to root yield.

The data of Table XIII are shown graphically in figure 7, in which the upper graph represents the variation among the individual cultures

in the ratio of dry weight of tops to dry weight of roots, while the lower graphs represent the corresponding variations in the water-requirements for roots, for tops, and for entire plants including both tops and roots.

TABLE XIII

WATER-REQUIREMENTS FOR TOPS, ROOTS, AND ENTIRE PLANTS, AND THE RATIO OF TOPS TO ROOTS: WHEAT GROWN FOR 24 DAYS IN SAND CULTURES AND SUPPLIED WITH A THREE-SALT SOLUTION HAVING A TOTAL OSMOTIC CONCENTRATION OF 1.75 ATMOSPHERES

| Culture Numbers | Water-Requirements ¹ | | | Ratio ² of Tops to Roots |
|-----------------|---------------------------------|-------|--------------|-------------------------------------|
| | Tops | Roots | Entire Plant | |
| R1 C1 | 237L | 1486 | 231 | 5.44 |
| C2 | 258L | 1160 | 211 | 4.49 |
| C3 | 255L | 1635 | 220 | 6.41 |
| C4 | 240L | 1401 | 205 | 5.82 |
| C5 | 298 | 1475 | 247 | 4.89 |
| C6 | 271L | 1480 | 229 | 5.47 |
| C7 | 280L | 1472 | 235 | 5.25 |
| C8 | 266L | 1568 | 227 | 5.91 |
| R2 C1 | 327H | 1116 | 253 | 3.41 |
| C2 | 293 | 1163 | 234 | 3.97 |
| C3 | 291 | 1375 | 240 | 4.73 |
| C4 | 277L | 1334 | 229 | 4.82 |
| C5 | 297 | 1072 | 233 | 3.61 |
| C6 | 282 | 1239 | 230 | 4.40 |
| C7 | 267L | 1173 | 217 | 4.40 |
| R3 C1 | 334H | 828 | 238 | 2.50 |
| C2 | 295 | 1031 | 230 | 3.94 |
| C3 | 291 | 1068 | 228 | 3.67 |
| C4 | 308 | 1181 | 244 | 3.84 |
| C5 | 291 | 1130 | 232 | 3.95 |
| C6 | 306 | 1618 | 258 | 5.28 |
| R4 C1 | 370H | 760 | 249 | 2.05 |
| C2 | 298 | 1038 | 232 | 3.48 |
| C3 | 326H | 1125 | 245 | 3.59 |
| C4 | 297 | 1247 | 240 | 4.20 |
| C5 | 307 | 1240 | 246 | 4.04 |
| R5 C1 | 348H | 976 | 256 | 2.80 |
| C2 | 323 | 1408 | 262 | 4.36 |
| C3 | 324 | 1403 | 263 | 4.33 |
| C4 | 325 | 1868 | 277 | 5.75 |
| R6 C1 | 308 | 1711 | 261 | 5.56 |
| C2 | 334H | 1773 | 282 | 5.29 |
| C3 | 378H | 1380 | 297 | 3.64 |
| R7 C1 | 332H | 1021 | 250 | 3.07 |
| C2 | 301 | 1266 | 243 | 4.21 |
| R8 C1 | 328H | 1040 | 249 | 3.14 |

¹ The water-requirement is determined by dividing the total water loss in grams by the dry weight value in grams.

² Obtained by dividing the dry weight of tops by the dry weight of roots.

The mean of the values for the water-requirements for tops is 307. It will be observed, in general, that the graph representing the ratio for tops (fig. 7) remains below the mean for the first twenty cultures, and that from this point forward the values equal or exceed the mean. From a study of the location of the cultures on the triangular diagram (fig. 8) it appears that a low water-requirement is associated with a low partial

osmotic concentration of mono-potassium phosphate. The location of each of the areas of high and of low water-requirements for tops is shown in figure 8, in which the area of high values is indicated by crosses and the area of low values is marked by small circles. As in case of dry weights, the shaded areas include the nine cultures showing the highest values and an equal number of cultures showing the lowest values. In Table XIII the nine cultures showing the highest water-requirements are marked H, while the nine showing the lowest water-requirements are marked L. The numerical values of the ratios for the different cultures are given on the diagram. A study of figure 9 with respect to water-

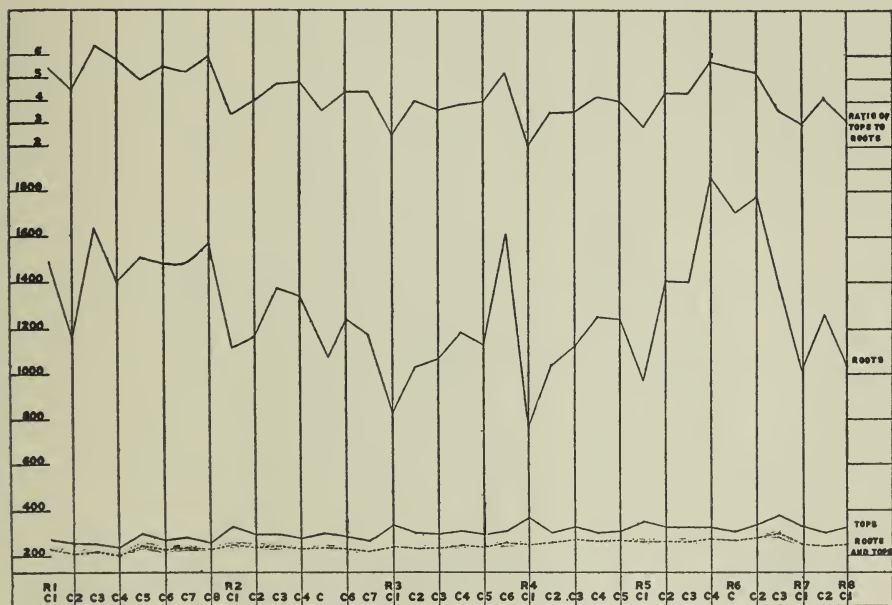


Fig. 7.—The water-requirement for the entire plant, for dry weight of tops and for dry weight of roots. The upper graph represents the variation in the ratios of tops to roots for the individual cultures.

requirements of the nine cultures giving the highest yield of tops and the nine cultures giving the lowest yields brings out the following facts. The average water-loss from the best nine cultures is 97 per cent greater than the water-loss from culture R1 C1, while the average yield of tops is only 89 per cent greater than that from culture R1 C1. The average water-loss from the poorest nine cultures is 27 per cent greater than that from culture R1 C1, while the average yield is 8 per cent greater than that from culture R1 C1. These observations are in accord with what might be expected from *a priori* grounds and from previous studies of water-requirement, namely, that favorable conditions for plant growth are generally associated with low water-requirements and that unfavorable conditions are concomitant with an increased water-requirement.

(c) Water-Requirement per gram of Dry Roots

The mean of the values for the water-requirements for dry weight of roots is 1285. It will be observed from the graph for this value in figure 7 that there is a region of high values near each end, with a distinct region of low values between. From a comparison of this graph with the graph representing the ratio of top yields to root yields it will be seen that the two lines follow each other quite closely. In every instance a

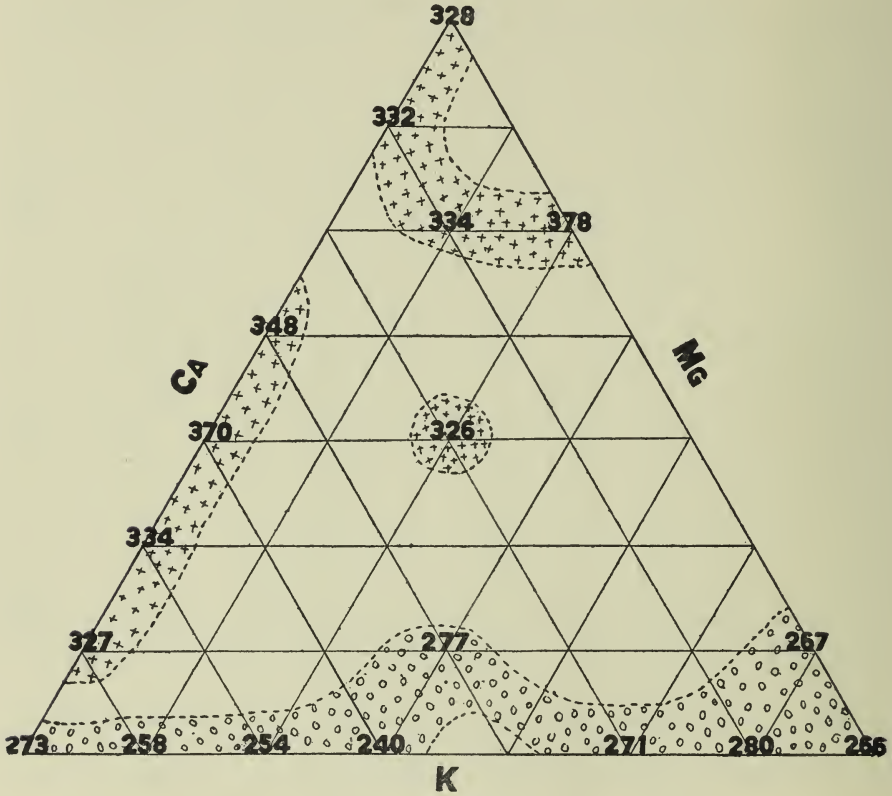


Fig. 8.—Areas of high and of low water-requirement values. The figures give the absolute values for 18 selected cultures.

high water-requirement corresponds to a high ratio of tops to roots and a low water-requirement corresponds to a low ratio of tops to roots. This is in harmony with what might be expected, since a high ratio of tops to roots suggests a large evaporating surface and a correspondingly high water-loss. As might be expected, the variation in the water-requirements is much greater for roots than for tops, the range for roots being from a minimum value of 760 (culture R1 C1) to a maximum value of 1868 (culture R5 C4).

(d) Water-Requirement per gram of Entire Plant

In figure 7 the graph representing the water-requirement for the entire plant very closely parallels the graph giving the ratios for dry weight of tops, and both show the same tendency to rise as we proceed from left to right. However, there are absent from the former the very high points that are characteristic of the graph representing the water-requirement for dry weight of tops, and that characterize those cultures having low ratios of tops to roots.

From an inspection of the graphs presented in figure 7 it is apparent that for this series of sand cultures the range of the water-requirement values, between the different cultures throughout the series, is comparatively narrow, when the dry weight of the plant is taken as the basis from which this ratio is derived. The range for the entire series of 36 cultures is from a minimum of 205 (culture R1 C4) to a maximum of 297 (culture R6 C3).

VI. *The effect of the Calcium-Magnesium Ratio upon the Growth Rate*

(a) Introduction

As the result of his investigations concerning the physiological requirements of plants, Loew (23) has worked out an hypothesis concerning the functions of lime and magnesia in the nutrition and the growth of plants. Early in these studies he became greatly impressed by the reversal of the quantitative relations of the lime and magnesia in the straw and in the seeds of plants. A chemical study of the ash of many common field plants brought out the fact that in the grain the magnesia is greatly in excess of the lime, while in the straw the lime is in excess of the magnesia. For example, in case of wheat, the ash of the grain contains 3.5 per cent of CaO and 13.2 per cent of MgO, while the straw has 5.8 per cent of CaO and only 2.5 per cent of MgO (39). His study of these data and the results of his own investigations led him to formulate the theory concerning the relationship of calcium to the nucleo-proteids and the specific function of magnesium with respect to the translocation of phosphorus in the plant. The outstanding points of Loew's lime-magnesia ratio hypothesis are as follows:

(1) When lime occurs in the growth medium greatly in excess of magnesia, or when magnesia occurs greatly in excess of lime, an injurious effect upon the plant is to be noted.

(2) Either of these elements tends to neutralize the harmful effects of the other.

The outstanding conclusions which Loew has drawn from his own and other experimental data are as follows:

(1) Different plants require, for their best growth, slightly different proportions of lime and magnesia.¹

¹ In practically all of the literature the results are discussed in terms of the ratio of CaO to MgO rather than the ratio of CaO to Mg, hence the use of the terms "lime" and "magnesia" in this paper.

(2) The optimum ratio of lime to magnesia for oats is 1:1, for barley 2:1, and for buckwheat 1:3.

Upon the basis of various physiological investigations the writer just mentioned recommended that the amount of available lime and magnesia should be determined in agricultural soils in order to ascertain the proper lime-magnesia ratio. In a later publication Loew (24) discusses the physiological functions of calcium and magnesium in the plant. According to this writer, the presence of lime is necessary for the formation of certain calcium compounds required in the nuclei and in the chlorophyll bodies of the plant, and that magnesia assists in the assimilation of phosphorus, since magnesium phosphate can give up its phosphoric acid more easily than any other phosphate that occurs in the plant sap. The element calcium, therefore, is fixed in the organized structure of the cells, while magnesium is movable and serves as a carrier of assimilable phosphoric acid, which rôle can be repeated several times. But, if lime is taken up in excess, the assimilation of phosphoric acid will be made more difficult, since the acid will combine with the lime and thus diminish the chances for the formation of magnesium phosphate. As a result of the excess of lime, therefore, the amount of available phosphoric acid may be reduced and the plant may experience a partial starvation. If, on the other hand, magnesia is in considerable excess, the calcium of the nuclei and chlorophyll bodies may be transformed in the presence of the soluble magnesium salts into magnesium compounds, by an exchange of bases. This transformation of the calcium nucleo-proteids changes their capacity for imbibition, much to the detriment of the plant. According to the law of mass action, however, this transformation may be prevented by the simultaneous presence of dissolved calcium salts.

Since the publication of the lime-magnesia hypothesis of Loew, many other investigators have published experimental results bearing on the question here brought up. In a recent paper, Lipman (17) gives a critical review of 64 papers, all of which report results bearing upon the hypothesis of the lime-magnesia ratio. Some of these results appear to support Loew's hypothesis, others are inconclusive, and a third group seem to cast very serious doubt upon the necessity for definite ratios of lime to magnesia for the best growth of plants. Of the 64 papers considered by Lipman, 24 claim to give positive evidence of the need for a definite lime-magnesia ratio in the soil; 26 report negative results; and the remainder make no claim to either positive or negative results. In much of this literature the experimental evidence is not conclusive nor convincing, since the results obtained may be explained without resort to the hypothesis of Loew. To quote from Lipman: "The toxic effects of magnesium in excess or when applied to the soil when not in excess are easily explained on the basis of its own specific physiological properties

and need no introduction of ratio considerations between itself and calcium to explain them. . . . Calcium and magnesium are, of course, essential elements in the growth of plants. Their somewhat similar chemical nature does not give us leave, however, to place them in a similar physiological category, and indeed numerous investigations point to their total dissimilarity, so far as that is concerned; Loew's own investigations being perhaps the most important in support of that idea. But, in spite of that, it is inconceivable to any one who has in view the modern developments of plant physiology and physical chemistry, as well as the modern views on the soil and its solution, why it should be any more assumed that a proper ratio between calcium and magnesium is necessary than that a proper ratio between calcium and potassium, and between calcium and iron, and between calcium and other essential elements in the growth of plants, are necessary. . . . The balance of the effects which are not accounted for by antagonism between the ions within the soil solution itself, may, so far as soils themselves are concerned, be just as easily explained on the basis of the effects of the applications on the physical conditions of the soil, on the chemical reactions following in the soil, on the bacterial flora, on the protozoan fauna, and on other fauna within the soil, as it can be, by introducing the rather far-fetched notion of the necessity of the lime-magnesia ratio."

It requires but a superficial examination of the literature to reveal the fact that, in a majority of the experiments heretofore carried out in this connection, no attempt has been made to differentiate between the purely physiological action of calcium and magnesium and what may be called their *environmental* effect. It has been found that, in certain soils where magnesia is in excess of lime, application of the latter substance has been very beneficial to the growth of crop plants. In such cases it is not necessary to suppose that the benefit comes from the correction of an unfavorable ratio between the calcium and magnesium. Indeed, it would seem just as plausible to assume that the good effect obtained is the result of the beneficial effect of the lime upon the bacterial flora of the soil, which effect may be so great as to obscure any physiological effects due to an improvement of the calcium-magnesium ratio, if such effects are actually present. In such a case, the addition of lime to the soil would be considered as affecting the bacterial environment of the plant, without reference to any direct effects produced upon the plant by the higher soil content of calcium.

The sand-culture method described in this paper seems to afford favorable conditions for studying the relation of the calcium-magnesium ratio to the growth of plants. The substratum of pure sand, in which the wheat plants of these studies were grown, furnishes physical conditions similar to those found in the open soil, but avoids many of the biological complications encountered with natural soils, which complications may

very readily obscure the physiological relations between the plant and the salts of its surrounding medium. Furthermore, the renewal of the nutrient solutions at the end of every 3-day period serves to maintain within the medium a fairly constant condition with respect to all of the salts contained in the solutions. If a definite value of the calcium-magnesium ratio is essential for the best development of the seedling, evidence of that fact should be expected from such a complete series of sand cultures as the one here employed, since one of the cation ratios (Mg/Ca) is very closely related to the much discussed lime-magnesia ratio. If, on the other hand, the physiological processes of the plant are dependent in this connection, upon the proper balancing of the solution as a whole, we should not expect to find here any definite correlation between the value of the calcium-magnesium ratio and the growth and development of the seedlings.

(b) Discussion of Data

Examination of the data presented by the diagram of figure 2, with respect to the osmotic proportions of calcium nitrate to magnesium sulphate in a number of selected cultures, brings out some points in this connection. In the culture giving the best growth of tops (R2 C7) the osmotic ratio of $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 is 7:1, while in the culture giving the poorest growth of tops (R4 C1) this ratio value is 1:5 (C.2:1.0). The average ratio of $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 for the best nine cultures has a value of 2.4:1, while for the poorest nine cultures this value is 1:2.9. It is thus evident that good growth is associated with a high osmotic ratio of $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 and that the poor cultures are characterized by a low value of this ratio. We are not justified, however, in drawing from these results, any definite conclusions with respect to the effect of the calcium-magnesium, as such, because of the fact that much of the superior growth, in the culture where $\text{Ca}(\text{NO}_3)_2$ is in excess, may be ascribed to the presence of a large amount of the NO_3 radical, which is known to be favorable to very vigorous vegetative growth.

It has long been known that most higher plants absorb the greater part of their nitrogenous food material in the nitrate form. Hellriegel and Wilfarth's (14) experiments with barley in sand cultures, where the nitrogen was supplied in the form of $\text{Ca}(\text{NO}_3)_2$, show a very marked increase in the amount of dry matter produced, as the amount of nitrogen is increased up to a certain maximum, above which additional increments of $\text{Ca}(\text{NO}_3)_2$ produce no further effect. It has been suggested by Russell (31) that the increasing effects produced by successive increments of nitrogen up to this maximum may be due to the fact that the additional nitrate not only increases the concentration of the radical in the solution, but that it also increases the extent of the absorbing surface of the roots and also that of the leaves. The process thus seems to bear some re-

semblance to autocatalysis, in which one of the products of the reaction serves as a catalyzer and hastens the reaction. This process, however, cannot go on indefinitely, because the time must come when some limiting factor will intervene and prevent further increase. Von Seelhorst (35) studied the effect upon the oat plant of the addition of nitrogen to soils containing different amounts of water. The experiment included 9 pot-cultures, which were divided into 3 series of 3 cultures each. In one series the soil used was just moist; in the second series the moisture content was slightly higher; while in the third series the soil was kept very moist. One pot in each series received no nitrogen, a second received 0.5 gm. of NaNO_3 , and the third received double that amount. In those cultures where only a small amount of moisture was present the addition of 0.5 gm. of nitrogen was without effect, the supply in the soil being sufficient for the needs of the plants, the water supply rather than the supply of nitrogen being the limiting condition. When more water was present the plants were able to make more growth and to utilize more nitrogen. The addition of one increment of nitrogen to the slightly moister soil of the second pot increased the produce by 10 gm., but the addition of the second increment was without additional effect, the water supply having again become the limiting condition. When a liberal amount of water was supplied, the first increment of nitrogen gave an increase of 20 gm., and the addition of another increment gave a still further increase of 15.5 gm.

In the present studies, where the moisture content of the soil was kept very nearly optimum, it might be expected that the dry weight of the plants would increase, with increase in the nitrogen content of the nutrient solution, until some condition other than water-supply became the condition limiting growth. Attention has been called to the fact that this series showed a gradual increase in the dry weight of tops in the cultures of row 1, as we proceed from C1, with 1 tenth of its total osmotic concentration due to $\text{Ca}(\text{NO}_3)_2$, to C8, with 8 tenths of its total concentration derived from that salt. As we pass upward toward the apex of the triangular diagram (fig. 2), however, the effect of additional increments of $\text{Ca}(\text{NO}_3)_2$ above the amount present in Culture C1 is not so apparent and soon entirely disappears except in the case of the first increment. The results obtained in this series suggest that, in the cultures represented as lying in the upper region of the diagram, the amount of KH_2PO_4 present in the solution may be the limiting condition, beyond the second culture from the left margin in each row.

The effect of the ratio of calcium nitrate to magnesium sulphate, upon the growth of tops, is brought out by an inspection of the cultures represented as occupying row 1, at the base of the triangular diagram (fig. 1). All of the cultures in this row have the same partial osmotic concentration of KH_2SO_4 ; namely, 1 tenth of the total osmotic concentration.

Passing to the right from culture R1 C1, the osmotic concentration of $\text{Ca}(\text{NO}_3)_2$ increases by increments of 1 tenth, up to a partial concentration of 8 tenths of the total, culture R1 C8. As the partial osmotic concentration of $\text{Ca}(\text{NO}_3)_2$ increases from left to right, that of MgSO_4 decreases at the same rate. With the exception of one culture (R1 C5), the dry weight of tops increases with increasing partial osmotic concentration of $\text{Ca}(\text{NO}_3)_2$, and with decreasing partial concentration of MgSO_4 . An inspection of harvest record (Table VI) shows that culture R1 C8, with the osmotic ratio, $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 , of 1:8 produced 100 per cent greater dry weight of tops than did culture R1 C1, where the value of the $\text{Ca}(\text{NO}_3)_2$ — MgSO_4 ratio was 1:0.12. The greatest difference between individual cultures is found in the case of cultures R1 C1 and R1 C2, where a decrease of one increment in the partial osmotic concentration of MgSO_4 and a corresponding increase in the partial osmotic concentration of $\text{Ca}(\text{NO}_3)_2$ resulted in an increase of 48 per cent in the yield of tops. Increases of a similar magnitude are found when cultures R2 C2, R3 C2, and R4 C2, are each compared with the first culture in its row.

Considering the culture occupying the right margin of the diagram (fig. 3, A), all of which had the same proportion of MgSO_4 , high yields of tops are associated with large osmotic partial concentrations of CaNO_3 and with low concentrations of KH_2PO_4 . Proceeding toward the upper apex of the triangle, beyond the second row, the dry weights decrease with decrease in the value of the ratio, $\text{Ca}(\text{NO}_3)_2$ to MgSO_4 . Osterhout (28) has pointed out that potassium may inhibit more or less completely the poisonous effect of excessive quantities of magnesium. Working with a marine alga (*Enteromorpha Hopkirkii*), he found these plants lived 5 times as long in a mixture of magnesium and potassium chlorides as in pure magnesium chloride, and 3 times as long as in pure potassium chloride. This same writer also grew wheat and other flowering plants in mixtures and in pure solutions of the same salts, with similar results. During a period of 40 days the wheat roots made a growth of 10 mm. in a .0937 m. MgCl_2 solution, but in a mixed solution (of the same total concentration) of KCl and MgCl_2 the growth was 153 mm. for the same time period. The results of the present investigation indicate that KH_2PO_4 is not effective in balancing the nutritive solution after a certain minimum ratio of calcium nitrate to magnesium sulphate has been reached. In this instance a marked decline in yield is shown between R2 C7 and R3 C6 as we go from a calcium nitrate to magnesium sulphate ratio of 7:1 in the former to a ratio of 6:1 in the latter.

It is obvious that if there is an optimum calcium-magnesium ratio value for the best growth of plants it can hold only within certain limits. For example, if the total concentration of the nutrient solution is too high, plants will fail to make satisfactory growth, whatever the

value of the calcium-magnesium ratio may be. Furthermore, the omission of KH_2PO_4 from the solution, or an addition of an excess of this salt, would make impossible the growth of plants in such a medium, regardless of any consideration of the calcium magnesium relation.

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PLATE I.

Wheat cultures about 20 days old, showing form of pot and arrangement for renewing the solutions. Scale is inches.



VITA

The writer was born at Buena Vista, Ohio, November 11, 1874. He attended the Southern Ohio Normal School, Manchester, Ohio, and taught in the public schools of Ohio from 1892 to 1896. In 1896 he entered the Ohio State University, graduating from this institution in 1900 with the degree of Bachelor of Science. The winter of 1900-1901 was spent in post-graduate work at the same institution. During the period from 1901 to 1904 he was Scientific Assistant in the Physical Laboratory, Bureau of Soils, United States Department of Agriculture, and from 1904 to 1906 Assistant Professor of Agronomy in the Ohio State University. From 1906 to 1916 he was Professor and head of the Department of Agronomy at the same institution. For the year 1914-1915, while on leave from the university, he was Fellow by courtesy and graduate student at the Johns Hopkins University.



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